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Species responses to climate change and landscape fragmentation: the central role of dispersal

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Contents

1 General Introduction

1 Climate change and landscape fragmentation: evidence and consequences for biodiversity

The climate is undoubtedly changing at an accelerated pace worldwide. The Intergovernmental Panel on Climate Change, in their fifth assessment report (IPCC, 2014), summarized the different components of climate change, their evidence, and their links with human activities. Global earth surface temperature showed a 0.85°C increase between 1880 and 2012. Moreover, the last 30 years (1983-2012) was the warmest period (90-100% of likelihood) over the last 800 years. The frequency of extreme events such as extreme warm temperature and extreme precipitation also increased in recent decades (IPCC, 2014). Global warming trends are predicted to be at least maintained or even exacerbated in the next century due to the increase in human induced greenhouse gas emissions (Santer *et al.*, 2013). Depending on the socio-economic contexts, models predict an increase in average surface temperature of 1.0 to 3.7°C in 2081-2100 relative to the 1986-2005 period (Figure 1.1, Table 1.1). Increasing temperatures are predicted to be associated with higher and longer extreme warm temperature events, a change in the water cycle and an increase in sea level. Past and future climate change affect human and natural systems in return, making climate change one of the main causes of biodiversity changes observed nowadays (Brooks *et al.*, 2002; Parmesan, 2006; Selwood *et al.*, 2015).

Contemporary climate change is already threatening biodiversity worldwide (Parme-

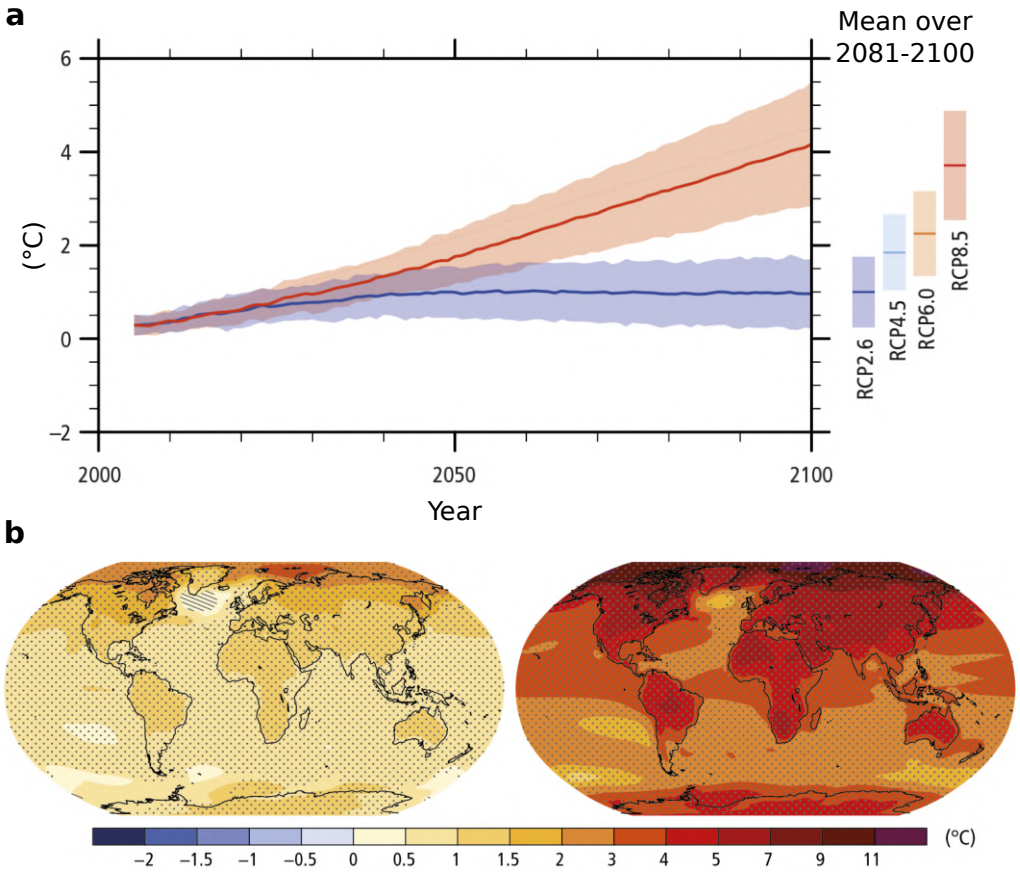


Figure 1.1 – Change in average global air temperature depending on different socio-economic scenarios (IPCC, 2014). **(a)** Global average surface temperature change from 2006 to 2100 relative to 1986–2005. **(b)** Change in average surface temperature for 2081–2100 relative to 1986–2005 under the RCP2.6 (left) and RCP8.5 (right) scenarios. Figure reconstructed from IPCC (2014).

Scenario	**2046 - 2065**	**2081 - 2100**
RCP2.6	1.0 [0.4-1.6]	1.0 [0.3-1.7]
RCP4.5	1.4 [0.9-2.0]	1.8 [1.1-2.6]
RCP6.0	1.3 [0.8-1.8]	2.2 [1.4-3.1]
RCP8.5	2.0 [1.4-2.6]	3.7 [2.6-4.8]

Table 1.1 – Projected change in global mean surface temperature (and 5 to 95% model range predictions) for the mid- and late 21st century, relative to the 1986–2005 period. Table reconstucted from IPCC (2014)

san, 2006; Selwood *et al.*, 2015; Urban, 2015, 2018). Both abiotic and biotic factors could lead populations to go extinct under climate change (Cahill *et al.*, 2013). Warming climate should indeed make temperature exceed thermal tolerances of most organisms (Deutsch *et al.*, 2008; Sinervo *et al.*, 2010). It could result in individual death due to overheating or it could restrict their period of activity. Individuals could indeed hide into cool

refuge to avoid overheating. However, the time spent into refuge limits time dedicated to other vital activities such as foraging. As a consequence, restriction in periods of activity could hamper major physiological functions (metabolism, growth rate, reproduction) and increase extinction risk (Sinervo *et al.*, 2010). Moreover, climate change can modify biotic interactions; for instance it could disrupt mutualistic interactions (Memmott *et al.*, 2007), promote competition and/or pathogens (Pounds *et al.*, 2006) and have a negative impact on beneficial species such as decreasing the amount of prey for a predator species (Memmott *et al.*, 2007). Even if evidence remains relatively scarce (Cahill *et al.*, 2013), population extinction has already been observed (Parmesan *et al.*, 1999; Wilson *et al.*, 2005; Pounds *et al.*, 2006; Thomas *et al.*, 2006; Pacifici *et al.*, 2017; Urban, 2018). Models forecasting future species distribution under climate change predicted the extinction of 5 to 37% of all species depending on the geographic location (Thomas *et al.*, 2004; Urban, 2015). Furthermore, these models predicted impacts of climate change on biodiversity without considering other elements of global change which may act in synergy with climate change (Opdam & Wascher, 2004; Brook *et al.*, 2008; Bellard *et al.*, 2015). Global change refers to changes in the earth system and encompasses changes in climate, land cover, pollution, sea level, urbanization, ocean cycles, carbon cycles.... Global change is commonly used to refer to changes associated with human activities (e.g. climate change, pollution, landscape fragmentation). Among them, landscape fragmentation is predicted to be the main threat to biodiversity in terrestrial area (Sala *et al.*, 2000; Jantz *et al.*, 2015).

Agriculture, deforestation and urbanization change the landscape structure. Important amount of natural habitats are lost and the remnant parts are split in small and isolated patches (i.e. landscape fragmentation, Wilcove *et al.*, 1986; Fahrig, 2003). Landscape fragmentation often gathers habitat loss (i.e. loss of sustainable habitat) and habitat fragmentation *per se* (i.e. the "breaking apart" of habitat independently of habitat loss; Fahrig, 2003). Landscape fragmentation impacts biodiversity by reducing patch size, increasing isolation and edge effects and altering patch shapes and matrix structure (Didham, 2010). Whereas habitat loss has a strong negative effect on biodiversity (e.g. Brook

et al., 2003), habitat fragmentation *per se* can have either positive or negative effects on biodiversity (Fahrig, 2017). For instance, reducing patch size decreases the number of species present in a given habitat (species-area relationship, e.g. Seabloom *et al.*, 2002). Habitat fragmentation *per se* also increases the proportion of edges for a given amount of habitat. Edges could increase population extinction as it promotes emigration of individuals into the unsuitable matrix (Fahrig, 2003). On the other hand, edges could be advantageous for particular species preferring warmer and drier conditions (Fahrig, 2003; Didham, 2010). Overall, habitat loss and fragmentation have been shown to reduce biodiversity by 13 to 75% (Haddad *et al.*, 2015) and could have a long lasting effect on future species persistence (i.e. extinction debt, Tilman *et al.*, 1994; Debinski & Holt, 2000; Krauss *et al.*, 2010; Dullinger *et al.*, 2012). Moreover, models predict further extinction due to the increase in fragmentation related to human activities (Pereira *et al.*, 2010; Jantz *et al.*, 2015).

Contemporary global change encompasses major threats to biodiversity. The different factors constituting global change act on their own and in synergy to affect populations, species, communities and ecosystem structure and functioning (Warren *et al.*, 2001; Opdam & Wascher, 2004; Jetz *et al.*, 2007; Brook *et al.*, 2008; Hof *et al.*, 2011; Comte *et al.*, 2016; Pereira *et al.*, 2010). For instance, Hof *et al.* (2011) projected the three major threats to amphibian diversity worldwide (climate change, landscape fragmentation and pathogens) and noticed that the different threats often co-occurred, making prediction regarding threats taken independently irrelevant. Moreover, the different drivers of species extinction often interact. For example, population decline of a rotifer species under experimental conditions was 50 times faster when different threats acted in synergy rather than independently (Mora *et al.*, 2007). Amphibian extinction in Costa Rica was also due to synergetic effects of different threats. Climate change is threatening amphibians on its own by increasing risk of overheat and desiccation. Moreover, climate change is also promoting a pathogen (*Batrachochytrium*), surging species extinction in this region (Pounds *et al.*, 2006). The different drivers of global change could also act in opposite directions. In the cooler part of their range, climate change could be beneficial for species.

However, landscape fragmentation could buffer or reverse the positive effect of climate change. Warren *et al.* (2001) observed a strong population decline of many butterfly species in the northern part of their range, where climate change was predicted to be beneficial, because of landscape fragmentation.

Landscape fragmentation could also buffer species responses to climate change (e.g. Opdam & Wascher, 2004). Species are indeed able to respond to climate change (i.e. range shift, phenotypic changes) through different mechanisms. These responses could buffer the effect of climate change on biodiversity. Nevertheless, landscape fragmentation might affect these responses and either limit or hamper species response to climate change (Warren *et al.*, 2001; Opdam & Wascher, 2004). A better understanding of how climate change and landscape fragmentation interact to shape future species distribution and composition is therefore one of the current major scientific challenges in ecology (Selwood *et al.*, 2015).

2 Responses to climate change in a fragmented landscape

2.1 Range shift and phenotypic changes

Two non exclusive responses may allow species to persist under climate change: range shift, and population phenotypic changes. Individuals can first follow through space the suitable climatic conditions, resulting in a change in the spatial distribution of populations (Parmesan & Yohe, 2003). Latitudinal and altitudinal shifts in response to climate change have been already recorded in different taxonomic groups (e.g. insects (Parmesan *et al.*, 1999), plants (Kelly & Goulden, 2008), fishes (Perry *et al.*, 2005)). Chen *et al.* (2011) measured that species are currently moving on average at a rate of 11 meters per decade in altitude and 16.9 kilometres in latitude in response to climate change. However, there is a strong variation among species in their rate of shift (Chen *et al.*, 2011; MacLean & Beissinger, 2017). Species traits could indeed modulate species range shifts under climate

change (Angert *et al.*, 2011; MacLean & Beissinger, 2017). Traits might shape the ability of individuals to colonize new habitats at the cold margin of the species distribution (Perry *et al.*, 2005; Pearson, 2006; Angert *et al.*, 2011; Schloss *et al.*, 2012; MacLean & Beissinger, 2017). For example, Schloss *et al.* (2012) predicted that 9.2 to 39% of mammal species may be unable to track suitable climatic conditions due to dispersal limitation in the northern hemisphere. However, as the different responses to climate change are non-exclusive, trait distributions could also change in response to climate change, and affect species range shift (Figure 1.2).

Populations could indeed respond to climate warming by changing their phenotypic composition without shifting their geographical range (Parmesan, 2006; Lavergne *et al.*, 2010). One of the main phenotypic changes observed in response to recent climate warming was phenological shift (Parmesan & Yohe, 2003; Réale *et al.*, 2003; Root *et al.*, 2003; Menzel *et al.*, 2006; Charmantier *et al.*, 2008; Massot *et al.*, 2017). Individuals advanced their spring events (e.g. breeding, laying date, flowering, budbursting) with increasing spring temperature (Parmesan & Yohe, 2003). Other phenotypic change, such as change in melanism (Roulin, 2014; MacLean *et al.*, 2019), body size (Daufresne *et al.*, 2009; Gardner *et al.*, 2011; Sheridan & Bickford, 2011), morphotype (Gibbs & Karraker, 2006) and physiology (Seebacher *et al.*, 2015) were also linked to climate change. In particular, climate change effects on life-history traits (i.e. survival, growth, reproduction and dispersal) could have important impacts on species responses to climate change as they result in change in population dynamics (Whitfield *et al.*, 2007; Ozgul *et al.*, 2010; Bestion *et al.*, 2015b). Climate-dependent population dynamics have been studied in different taxonomic groups (e.g. insects (Deutsch *et al.*, 2008), birds (Jenouvrier *et al.*, 2018), mammals (Ozgul *et al.*, 2010), reptiles (Le Galliard *et al.*, 2010)) and encompass changes in population density, age and size structure (Whitfield *et al.*, 2007; Daufresne *et al.*, 2009; Cunningham *et al.*, 2017). For instance, climate change affects population size structure and/or age structure in ectotherms toward smaller and younger individuals (Daufresne *et al.*, 2009; Gardner *et al.*, 2011; Sheridan & Bickford, 2011). In fish populations, climate change positively affects body growth and survival of small individuals while it has

negative effects on the survival of bigger individuals, affecting population size structure (Vindenes *et al.*, 2014). Change in life-history traits also influences demography by determining population density. As evolutionary and demographic processes are closely linked (i.e. eco-evolutionary dynamics (Le Galliard *et al.*, 2005a; Kokko & López-Sepulcre, 2007; Schoener, 2011)), population density could affect the phenotypic response of population to climate change (Figure 1.2). For instance a decrease in population density could increase the strength of genetic drift, reduce the efficiency of selection, and lead to the fixation of deleterious mutations in the population. As a result, mean population fitness should be reduced, leading to further reductions in population size (Legrand *et al.*, 2017). Changes in population dynamics could therefore affect the relative influence of the processes behind population phenotypic changes, namely phenotypic plasticity and evolutionary adaptation.

Phenotypic plasticity is the ability of a genotype to produce different phenotypes in different environments (Pigliucci, 2001, 2005). Plasticity could thus modify population phenotypic distribution without any change in allele frequencies. Climate driven phenotypic changes due to phenotypic plasticity have been observed in many studies (reviewed by Boutin & Lane, 2014; Charmantier & Gienapp, 2014; Crozier & Hutchings, 2014; Franks *et al.*, 2014; Reusch, 2014; Schilthuizen & Kellermann, 2014; Stoks *et al.*, 2014; Urban *et al.*, 2014). For example, great tit populations in the UK plastically advanced their laying date in response to warmer spring temperature (Charmantier *et al.*, 2008). Plasticity allows a fast response to environmental changes. However, the range of phenotype which can be produced by plasticity is not infinite. Moreover, plasticity could be costly to develop (DeWitt *et al.*, 1998). Plasticity could therefore fail to continuously produce phenotypes able to cope with continuously changing environment (DeWitt *et al.*, 1998). Furthermore, climate change could modify the link between reaction norm and fitness, making initially adaptive plastic changes maladaptive (Visser, 2008; Charmantier & Gienapp, 2014). For instance, breeding time in bird could be influenced by temperature as temperature determined the period of higher abundance of caterpillar for their chicks. However, if the correlation between caterpillar abundance and temperature is modified,

plastic response of bird to temperature will become maladaptive (Visser, 2008).

Evolutionary adaptation affects population phenotypic distribution through changes in allele frequencies. Under climate change, some genotypes produce phenotypes better adapted than others to the new climatic conditions and should be favored by natural selection. Evolutionary adaptation could be fast enough to play a role in population responses to contemporary climate change. For example evolutionary adaptation accounted for 13% of the advance in the breeding timing of Canadian populations of red squirrels in response to increasing spring temperature (Réale *et al.*, 2003). The capacity of a population to respond to climate change though evolutionary adaptation should depend on its genetic diversity; the higher the genetic diversity, the higher the probability for an allele adapted to the new climatic conditions to be present. Population density could also play a central role as it will determine the strength of genetic drift that could hinder evolutionary adaptation, and the probability for a new mutation to appear. Phenotypic plasticity could also affect (positively or negatively) evolutionary adaptation (Crispo, 2008).

Phenotypic plasticity and evolutionary adaptation are indeed closely related (Figure 1.2). Historically, phenotypic plasticity was thought to hinder evolutionary adaptation by buffering the selective pressures able to select optimum genotypes (DeWitt *et al.*, 1998). However, phenotypic plasticity has been demonstrated to promote evolutionary adaptation (e.g. Price *et al.*, 2003). Plasticity could indeed allow individuals to fast adapt to a new environmental condition and then evolutionary adaptation could replace phenotypic plasticity, for instance, if plasticity is costly to maintained (Conover & Schultz, 1995). Phenotypic plasticity can also be maladaptive and bring phenotypes to the wrong direction regarding the environmental conditions. In this case, evolutionary adaptation could be favored. Evolutionary adaptation could also directly act on phenotypic plasticity. Phenotypic plasticity has been demonstrated to be heritable and susceptible to evolve (Scheiner, 1993; Pigliucci, 2005; Crispo *et al.*, 2010). Evolutionary adaptation could thus favor or hinder phenotypic plasticity depending on the costs associated with plasticity (DeWitt *et al.*, 1998), the spatio-temporal variability in the climatic conditions and if plasticity is adaptive or maladaptive (Crispo, 2008; Crispo *et al.*, 2010; Gibbin *et al.*,

2017). The link between plasticity and evolutionary adaptation could also be shaped by dispersal and gene flow (Figure 1.2). Among its effects on species responses to climate change (see below), dispersal could indeed affect the genetic composition of populations, modifying the potential for evolutionary adaptation, and favor phenotypic plasticity as dispersers susceptible to persist under different environmental conditions will be advantaged (Sultan & Spencer, 2002).

2.2 Central role of dispersal in species response to climate change

Dispersal, the movement of individuals from birth site to breeding site or between two breeding sites (Howard, 1960), plays a central role in species response to climate change. Dispersal affects both range shift and population phenotypic change (Figure 1.2). Dispersal allows the colonization of new habitat made available by climate change, and thus species range shift. Dispersal also induces a gene flow among populations which can further modulate the evolutionary adaptation to climate change (Figure 1.2, Lavergne *et al.* (2010)). Individuals arriving into a population could bring either adaptive or maladaptive genes, promoting and swamping local adaptation respectively (Lenormand, 2002). Theory predicts that the swamping effect of dispersal from core populations to margin populations could limit species distribution (Bridle & Vines, 2007), and could compromise persistence under climate change (Pease *et al.*, 1989; Polechová *et al.*, 2009). More precisely, dispersal could either accelerate the phenotypic shift toward phenotypes better adapted to warmer conditions by bringing pre-adapted genotypes (at the cold margin mostly) or limit adaptation through a continuous flow of maladapted individuals (at the warm margin mostly). At a finer scale, gene flow among populations inhabiting different microclimates could affect metapopulation dynamics and compositions. Dispersal affects population density and its link to evolutionary processes (Figure 1.2). Moreover, whereas climate warming is not homogeneous through the landscape (Ashcroft *et al.*, 2009), habitats less affected by climate warming may act as source populations allowing the rescue of nearly extinct populations through dispersal (Pearson, 2006; Hannah *et al.*, 2014; Lembrechts *et al.*, 2018). Conversely, less affected populations may limit population adaptation to warmer

conditions by continuously sending maladaptive genes into the most affected populations.

As already mentioned at the end of the previous section, dispersal could modulate the link between evolutionary adaptation and phenotypic plasticity (Figure 1.2). Dispersal should shape the relative importance of evolutionary adaptation and phenotypic plasticity in population phenotypic changes in response to climate change. First, by allowing spatial range shift, dispersal could hamper selective pressures on phenotypes and help catch up with suitable climatic conditions rather than population phenotypic changes, reducing both plastic and evolutionary responses. Second, dispersal could reduce evolutionary adaptation by promoting phenotypic plasticity. In presence of random dispersal, Sultan & Spencer (2002) demonstrated that plastic individuals were favored compared to specialist and non plastic individuals. Dispersal should therefore promote the evolution of high phenotypic plasticity in heterogeneous environments (Crispo, 2008). Individuals should therefore be prompter to respond plastically to environmental perturbation, such as climate change. Furthermore, persistence of dispersers, whatever their genotypes, due to phenotypic plasticity should swamp local genetic adaptation (Lenormand, 2002). Conversely, dispersal on its own can be regulated by evolutionary processes. In the case where plasticity is reduced, selection could act against dispersers, when dispersal is random, as their probability to persist in a new environment is lower than resident individuals (Crispo, 2008). In that case, evolutionary adaptation could be favored.

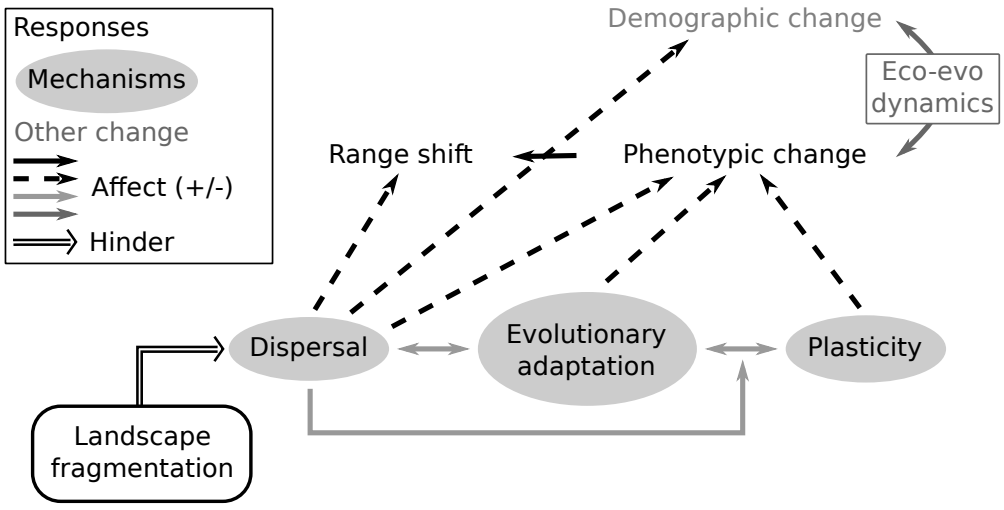


Figure 1.2 – Global synthesis of the links between the population responses to climate change, their underlying mechanisms and landscape fragmentation

However, all these predictions rely on the fact that dispersal is considered as random. Dispersal, though, is increasingly recognized to be a non-random process (Clobert *et al.*, 2001; Bowler & Benton, 2005; Edelaar *et al.*, 2008; Clobert *et al.*, 2009, 2012; Edelaar & Bolnick, 2012; Travis *et al.*, 2012; Lowe & McPeek, 2014). Dispersers are often characterized by a combination of traits promoting movement (i.e. dispersal syndrome, Clobert *et al.*, 2009; Ronce & Clobert, 2012; Cote *et al.*, 2017). The different stages of this process (i.e. departure, transience and settlement) are influenced by individual phenotype, local context and often their match (i.e. matching habitat choice). Variation in the phenotype of individuals may imply variation of fitness in specific environments which should select for inter-individual differences in emigration and immigration decisions according to their fit to local environmental conditions (Edelaar *et al.*, 2008). In contrast to random dispersal, where individuals move independently of their fitness expectation, individuals are expected to move from habitats where they expect a low fitness and to settle in habitats where they expect a higher fitness, making dispersal an adaptive process. Non-random dispersal, and matching habitat choice in particular, has been demonstrated in various species (e.g. insects (Karpestam *et al.*, 2012); fishes (Bolnick *et al.*, 2009); birds (Dreiss *et al.*, 2012; Camacho *et al.*, 2016; Benkman, 2017); reptiles (Cote & Clobert, 2007b; Cote *et al.*, 2008)), for different phenotypic traits matching different environmental conditions. For example, in three-spine sticklebacks *Gasterosteus aculeatus*, a mark–transplant–recapture experiment showed that dispersers' preferences for lake and stream habitats depended on lake-like and stream-like morphological attributes (Bolnick *et al.*, 2009). Moreover, a recent study demonstrated that dispersal decisions of an ectotherm species depend on the match between individuals' phenotype and climatic conditions (Bestion *et al.*, 2015a).

Under variable environmental conditions, matching habitat choice and ensuing adaptive gene flow may locally promote an efficient shift in mean populations' phenotypes and therefore may influence species' responses to climate change (Edelaar & Bolnick, 2012). Non-random dispersal and ensuing adaptive gene flow could also modify the expected links between phenotypic plasticity, evolutionary adaptation and dispersal. As individu-

als should move into habitat where they are adapted, the benefit of phenotypic plasticity should be reduced (Scheiner, 2016) whereas genetic adaptation should be favored. In that case, matching habitat choice can be seen as a plastic response, where individuals are able to adjust their position in space according to their phenotype and the local environment, rather than adjusting their phenotype (i.e. phenotypic plasticity). Furthermore, as climate warming is expected to increase local mismatch between individual phenotypic optimum and local temperature, matching habitat choice may make movements towards more suitable climatic conditions easier and promote an efficient shift of species geographic distribution (Edelaar & Bolnick, 2012).

2.3 Impacts of landscape fragmentation on dispersal and species responses to climate change

Landscape fragmentation limits dispersal (Figure 1.2) by decreasing the probability for individuals to find a suitable habitat and increasing their mortality during transience (Johannesen *et al.*, 2000; Fahrig, 2003; Bonte *et al.*, 2012). Furthermore, landscape fragmentation could reduce the adaptiveness of gene flow by hindering the optimality of dispersal decisions. Fragmentation indeed magnifies dispersal costs and should therefore hamper the exploration of surrounding habitats, reducing the optimality of dispersal decisions (Jacob *et al.*, 2015a; Cote *et al.*, 2017). As a consequence, landscape fragmentation could affect the two responses to climate change developed earlier in this section (i.e. range shift and population phenotypic changes). In fragmented landscapes, individuals may fail to follow the suitable climatic conditions, limiting the potential for species range shift (Warren *et al.*, 2001; Opdam & Wascher, 2004; Selwood *et al.*, 2015; Fourcade *et al.*, 2017). During climate change, fragmentation may also prevent individuals to access microclimatic refuges which could avoid individuals to suffer from extreme climatic conditions (Scheffers *et al.*, 2014; Suggitt *et al.*, 2018). As a result, landscape fragmentation may strengthen the climatic impacts on populations. Finally, landscape fragmentation should reduce gene flow among populations, limiting the input of new genotypes which could be selected for and hindering the beneficial effect of adaptive gene flow on genetic

adaptation.

Landscape fragmentation should thus affect species responses to climate change by modifying the relative influence of the different mechanisms behind these responses. By limiting spatial range shift, landscape fragmentation could raise extinction risk (Warren *et al.*, 2001; Opdam & Wascher, 2004; Jetz *et al.*, 2007; Brook *et al.*, 2008; Hof *et al.*, 2011; Comte *et al.*, 2016; Pereira *et al.*, 2010). Population persistence will then rely mainly on population phenotypic change. The relative influence of phenotypic plasticity, evolutionary adaptation and dispersal on population phenotypic change will also be shaped by landscape structure. By hampering dispersal, landscape fragmentation should enhance selective pressures on phenotypes as individuals could not escape from the stressful environmental conditions. The relative influence of phenotypic plasticity and evolutionary adaption will then depend on the genetic diversity, the capacity for plasticity, the cost associated with this plasticity and whether plasticity is adaptive or maladaptive. Development of studies tackling how landscape fragmentation modifies the relative influence of the different mechanisms behind species responses to climate change is urgently needed to better predict the future of biodiversity in the face of anthropogenic perturbations.

3 How to study species response to climate change in fragmented landscape

Complementary approaches can be used to study species response to climate change. Long term study of natural populations is often used to observe the consequence of climate change on populations (e.g. Réale *et al.*, 2003; Charmantier *et al.*, 2008; Massot *et al.*, 2017; Lane *et al.*, 2018). Such studies benefit from large datasets allowing to quantify precisely impacts on populations and to distinguish between plastic and evolutionary responses though the use of quantitative genetic approaches (Kruuk *et al.*, 2014). However, long term datasets are rare and require important time investment and fieldwork survey. Spatial studies regarding the link between climatic conditions and population composition and dynamics could also be used to predict the consequence of climate change in

a space-for-time substitution (e.g. Skelly & Freidenburg, 2000; Kealoha Freidenburg & Skelly, 2004). For example studies of different populations distributed on a latitudinal or altitudinal gradient could help understand how population compositions are shaped by the local climatic conditions and could be extrapolated to a context of climate change. However, space-for-time substitution induces other biases; studies along altitudinal gradient may, for instance, fail to distinguish between pressures induced by temperature and oxygen concentration. In a context of global change, using studies of natural populations to assess species responses to multiple drivers (e.g. climate change and landscape fragmentation) could be hard to accomplish. For instance, to study population responses to climate change and landscape fragmentation, it would require the survey of different populations inhabiting landscapes more or less fragmented to be able to distinguish the effect of each driver and their interaction. Studies of natural population indeed often fail to distinguish between the effects of different drivers of global change on populations. These studies could also suffer from the limited number of replicated sites. Experimental approaches could be an easier way to study combined drivers of global change.

Experimental approaches allow to test for the combined influence of climate change and other drivers of global change on biological systems, by manipulating these drivers in a crossed design. Experiments manipulating climatic variables have already been developed in many taxa (e.g. Benedetti-Cecchi *et al.*, 2006; Wernberg *et al.*, 2012; Wolkovich *et al.*, 2012; Bestion *et al.*, 2015a,b; Davenport *et al.*, 2017). Moreover, experiments could help distinguish between plastic and evolutionary responses to climate change (i.e. experimental evolution, transplant experiment, common garden experiment (Merilä & Hendry, 2014)). For instance, experimental evolution allows to directly link the observed phenotypic change to the conditions which have been manipulated rather than using correlative approaches. Moreover, it often allows to manipulate multiple drivers of global change simultaneously (e.g. Davenport *et al.*, 2017). Different methods can be used to distinguish between evolutionary adaptation and phenotypic plasticity in experimental evolution. The use of quantitative genetic approaches can be used if the pedigree of the individuals is known. Common garden experiment can also determine if the experimental treatments

led to evolutionary adaptation. Common garden experiment consists in raising individuals from different populations/conditions into standardized and common laboratory or field conditions (Merilä & Hendry, 2014). If the difference among populations/conditions remain after at least one or two generations of common garden (to minimize interference from maternal effects and acclimation (Stoks *et al.*, 2014)), we can conclude that evolutionary adaptation played a role in population differentiation. However, experiments are often limited in space and time. It could be thus difficult to make clear predictions on the long-term effect of global change on biodiversity with experiments only. The development of theoretical models, integrating parameters extracted from experiments, could then be needed.

Theoretical models could either be used to predict future distribution of particular species (e.g. bioclimatic envelop models (Thuiller *et al.*, 2005)) or to test for the influence of specific mechanisms in species response to climate change (e.g. biotic interactions (Bocedi *et al.*, 2013); pollen dispersal (Aguilée *et al.*, 2016)). Models allow to make predictions on large spatio-temporal scales, according to different climatic scenarios, landscape structures and species characteristics (e.g. Thomas *et al.*, 2001). Models could also be used to develop theoretical predictions, which could be validated (or invalidated) with the use of data on natural populations. The coupling of approaches is thus often needed to make reliable predictions and override the limits of each approach.

Especially, the coupling of models and experiments could be used in two different ways; experiments could be performed following model development to validate theoretical predictions (e.g. Fronhofer *et al.*, 2017); experiment could also precede model development. Experiment could indeed bring light on biological mechanisms which could be then integrated into a model to test their influence on larger spatio-temporal scales (e.g. Jacob *et al.*, 2018). Under climate change, significant improvements are needed to better predict future species distribution (Urban *et al.*, 2016). Experiments could help increase our knowledge on the interacting effect of climate change and habitat fragmentation on species persistence. For instance, the relative influence of dispersal, phenotypic plasticity and evolutionary adaptation in population response to climate change could be experimentally

tested. Mechanisms of dispersal and its influence on population adaptation, range shift and species persistence, depending on landscape configuration, could then be explored theoretically to provide more reliable predictions and set up efficient management policies and conservation plans.

4 Objectives

My PhD project aimed at improving our understanding on species responses to the combined effect of climate change and landscape fragmentation. I was especially interested in how dispersal, shaped by landscape structure, could affect species responses to climate change and modulate population adaptation to new climatic conditions. In 2015, Elvire Bestion defended her PhD thesis entitled "Impacts of climate change on a vertebrate ectotherm: from individuals to the community". During her PhD, she performed experiments on the common lizard and demonstrated that during one-year long experiment, a 2°C warmer condition accelerate the pace of life of individuals and may affect population persistence when these populations were isolated (Bestion *et al.*, 2015b). However, a longer period of time is required to assess the effect of accelerated pace-of-life syndrome on population dynamics. The accelerated pace-of-life syndrome, if maintained on a longer period of time, should lead to changes in the age and size structure of populations. However, evolutionary and plastic processes could enhance or buffer the accelerating effect of warmer temperature on individual pace of life and change the predictions about population dynamics. I therefore tested, as a first empirical objective, how climatic conditions influence population dynamics (Chapter 2) and population adaptation (Chapter 3) using a 3-years long experiment.

My second objective was to study how the connectivity among habitats could modulate the impacts of climatic conditions on population dynamics and adaptation. Landscape connectivity may change the effect of climate change in different ways. First, landscape connectivity allows the movements between microclimates, which may constitute microclimate refuges and slow down the impacts of climate change on population dynamics. Second, it allows a gene flow between habitats which adds up to the two other mech-

anisms underlying population adaptation, phenotypic plasticity and evolutionary adaptation. The relative influence of these 3 mechanisms in population response to climate change is still poorly studied. Moreover, common lizard has been demonstrated to perform matching habitat choice (Bestion *et al.*, 2015a). Matching habitat choice should thus promote population adaptation to local climate in connected landscapes (Edelaar & Bolnick, 2012; Bolnick & Otto, 2013; Scheiner, 2016; Edelaar *et al.*, 2017). Landscape fragmentation should alter the relative influence of evolutionary adaptation and phenotypic plasticity on population response to climate change by preventing dispersal. I used an experimental approach to study how evolutionary adaptation, dispersal and phenotypic plasticity shape population phenotypic response to different climatic conditions. To do so, I manipulated the connectivity between habitats to understand how connectivity between microclimates could modify the effect of climate on population dynamics (Chapter 2) and to quantify the role of the different mechanisms involved in population phenotypic change (Chapter 3).

My third objective was to understand how matching habitat choice could modify species response to climate change on large spatio-temporal scales. Matching habitat choice linked to climatic conditions, as demonstrated in Bestion *et al.* (2015a), could strongly affect species response to climate change. Under stable environment, previous models predicted that matching habitat choice should promote adaptive gene flow (Holt, 1987; Jaenike & Holt, 1991; Ruxton & Rohani, 1999; Armsworth & Roughgarden, 2005b, 2008; Bolnick & Otto, 2013; Scheiner, 2016) and favor population adaptation and differentiation on small spatiotemporal scales (Edelaar & Bolnick, 2012; Bolnick & Otto, 2013; Scheiner, 2016; Edelaar *et al.*, 2017). Under climate change, matching habitat choice could also promote an efficient shift of species geographic distribution (Edelaar & Bolnick, 2012), increasing species persistence. However, this verbal prediction has never been tested. I used a modeling approach to test how matching habitat choice modifies predictions of future species distribution under climate change (Chapter 4).

5 General methods

To reach these objectives, I used a combination of approaches allowing both to understand how populations respond to climate change in fragmented or continuous landscape and to test for the influence of matching habitat choice on species persistence under climate change. I used experimental and modeling approaches to tackle these questions.

5.1 The experimental approach

I used experiments to study population responses to climate change in fragmented and continuous landscape (chapter 2 and 3). The use of experiments allows to manipulate the drivers of interest rather than using correlative approaches. Moreover, it helps to distinguish between the processes behind population responses to climate change. Merilä & Hendry (2014) reviewed the methods which could be used to distinguish evolutionary adaptation from phenotypic plasticity. Among these methods, the use of experimental approaches such as experimental evolution and common garden experiments are of central interest to better understand how selective pressures and plasticity shape phenotypic responses to climate change. Moreover, landscape structure can be "easily" manipulated to test for the influence of dispersal on population response.

I performed a 3-years long experiment using populations of the common lizard (*Zootoca vivipara*) subjected to different climatic conditions and connectivity treatments. During three years, populations were inhabiting enclosures of an experimental system, the Metatron, allowing to manipulate climatic conditions and connectivity among populations. We monitored population composition and dynamics through time and measured evolutionary and plastic processes as well as dispersal. After the three years of treatments, the individuals were redistributed among the climatic conditions to test whether changes regarding the treatments induced advantages in the different climatic conditions.

The common lizard

The common lizard (*Zootoca vivipara*, Figure 1.3) is a small viviparous lacertid (adult snout-vent length = 50-70 mm). Its dorsal coloration is highly variable, ranging from light to dark brown, with some green reflects, and its ventral coloration ranges from pale yellow to dark orange. It spreads across Eurasia, from Ireland to Japan and northern Spain to Scandinavia (Figure 1.4), and can be found from sea level to high altitude (2900m (Agasyan *et al.*, 2010)). It inhabits a great variety of habitats including grassland, meadows, humid scrubland, hedgerows, open woodland, woodland edges, peat bogs, stream edges, coastal areas and rural gardens (Agasyan *et al.*, 2010) and feeds on a great variety of prey including spiders, Coleoptera, Orthoptera, Heteroptera, Homoptera, Diptera, Hymenoptera, Gasteropods, Isopods and Lepidoptera caterpillars, with Aranae, Orthoptera, Heteroptera and Homoptera being its favorite preys (Avery, 1966; Pilorge, 1982; González-Suárez *et al.*, 2011). The average lifespan of this species is five years (Sorci & Clobert, 1999) but females can reach up to 11 year-old and males up to 7 year-old (Richard *et al.*, 2005). Three age stages can be distinguished: juvenile (<1 year-old), yearlings (1 to 2 year-old) and adults (>2 year-old). Most natural populations are composed of ovoviviparous individuals, except some populations in the southern portion of the range which are oviparous (Surget-Groba *et al.*, 2006). Reproduction is mainly made by > 2 year-old individuals (Massot *et al.*, 1992), even if yearlings can also reproduce depending on their body size (Richard *et al.*, 2005; Bestion *et al.*, 2015b).

Common lizards hibernate from November to February in our study system (Ariège, France). Males emerge from hibernation one or two weeks before yearlings and females and mating starts right after females' emergence. Female reproduce with up to 7 males and males reproduce with up to 12 females (Richard *et al.*, 2005; Eizaguirre *et al.*, 2007). Gestation time depends on external temperature, but lasts generally two to three months. Females lay around 5 (1-12) soft-shelled eggs (Massot *et al.*, 1992). Parturition starts in June and all parturition occurred in a period of one month on average. Juveniles emerge from the eggs within one hour after parturition and are directly independent (Massot *et al.*, 1992). At birth, juveniles measured 21 ± 1 mm (snout-vent length) and weigh 0.19

Figure 1.3 – Lizards thermoregulating into an enclosure of the Metatron. a,e,f) Juvenile individuals, b) adult male individuals and c,d) adult female individuals. The female in picture d) finishes moulting

Figure 1.4 – Distribution area of the common lizard *Zootoca vivipara*. Source: IUCN spatial distribution data

± 0.03g in our experiment. There is a high mortality during the juvenile stage as 75% of juveniles die the first year.

Individuals disperse mostly at the juvenile stage (Le Galliard & Clobert, 2003), but yearlings and adults also disperse to a lower extent. Adult home range of common lizard is around 20 meters (Clobert *et al.*, 1994), and dispersal distance varies between 19 and 100 m (Clobert *et al.*, 1994, 2012). In this species, dispersal has been shown to be influenced by extrinsic factors (e.g. density (Clobert *et al.*, 1994; Le Galliard & Clobert, 2003; Cote & Clobert, 2007b), temperature (Massot *et al.*, 2008), kin competition (Cote & Clobert, 2007b, 2010)), intrinsic factors (e.g. body size (Clobert *et al.*, 1994; Cote & Clobert, 2010), maternal effects (Clobert *et al.*, 1994; Cote & Clobert, 2010, 2007b), social traits

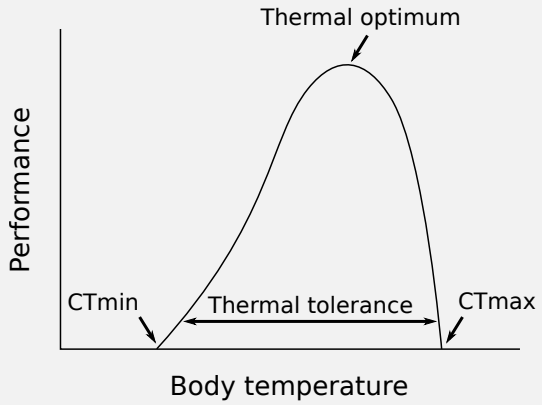
(Cote & Clobert, 2007b), stress level (Meylan *et al.*, 2002, 2004)) and their interaction (e.g. social behavior and local density (Cote & Clobert, 2007b)).

The common lizard, as all ectotherms, is dependent on external temperature for its physiological functions (Box 1). Physiological traits as well as morphological and behavioral traits associated with thermoregulation are therefore expected to be affected by contemporary climate change. For instance, the different parameters of thermal performance curve (Box 1) are crucial parameters for species persistence under climate change. However, their measurements can be challenging, in particular in studies examining the evolutionary and plastic processes behind phenotypic changes, as phenotype has to be measured at the individual level. Proxies for evaluating thermal performance are thus often used to characterize thermal physiology of ectotherms. In lizards, maximal critical thermal limit ($CTmax$), mean body temperature of active lizards in the field and preferred temperature in a laboratory thermal gradient are good proxies of thermal optimum (Huey *et al.*, 2012). Particular phenotypic and behavioral traits could also play a major role in buffering the influence of climate change on ectotherms' body temperature. For instance, Sinervo *et al.* (2010) predicted that the increase in external temperature should reduce the period of activity of lizards, leading to 39% of population extinction within species ranges. Behavioral adjustment may allow individuals to change their period of activity to avoid the warmest hours of the day and keep enough activity period for foraging and others important physiological functions. Individuals could adjust their period of activity by advancing their phenology or adjusting their period of activity within a day. Some morphological characteristics are also known to have a direct effect on body temperature of ectotherms. For instance, the darkness of the individuals affects their body temperature as darker individuals should be more at risk of overheating than paler ones (thermal melanism hypothesis (Trullas *et al.*, 2007)). Focusing on these traits could thus help predict ectotherm responses to contemporary climate change.

Effect of climate change on common lizard populations have been studied using long term monitoring of natural populations (Chamaillé-Jammes *et al.*, 2006; Massot *et al.*, 2008; Lepetz *et al.*, 2009; Le Galliard *et al.*, 2010; Rutschmann *et al.*, 2016; Massot *et al.*,

2017) and experimental manipulation (Bestion *et al.*, 2015a,b, 2017). In natural populations of the Cévennes mountains, warmer temperature affected population dynamics by promoting body growth, adult body size and clutch size (Chamaillé-Jammes *et al.*, 2006; Le Galliard *et al.*, 2010), advancing laying date (Le Galliard *et al.*, 2010; Massot *et al.*, 2017), reducing dispersal of juveniles (Massot *et al.*, 2008) and disturbing reproductive tradeoffs (Rutschmann *et al.*, 2016). Warmer temperature also affected phenotypic traits into populations; dorsal pattern distribution changed in response to climate warming (Lepetz *et al.*, 2009). Furthermore, one year experimental manipulations of climatic conditions highlighted the effect of warmer climate on life-history traits; warmer temperature accelerated individual pace of life (Bestion *et al.*, 2015b) and affected dispersal patterns through its influence on matching habitat choice (Bestion *et al.*, 2015a). Finally, warmer climatic conditions decreased the diversity of the gut microbiota of lizards (Bestion *et al.*, 2017). All these studies highlight the multiple facets of common lizards' responses to climate change. More efforts have to be done to better understand how future climatic conditions will shape population dynamics and composition of this species, and of all ectotherms in general, in the context of current global change. I aimed at doing so by using an experimental approach with populations maintained for several generations and manipulating simultaneously climatic conditions and connectivity among habitats.

Box 1: Thermal physiology of ectotherms in the face of climate change



Ectotherm body temperature is directly linked to external temperature and shapes all the behavioral and physiological traits (Angilletta *et al.*, 2002), such as metabolism (e.g. Gillooly *et al.*, 2001; Brown *et al.*, 2004; Dillon *et al.*, 2010), locomotion (e.g. Bennett, 1990), digestion (e.g. Van Damme *et al.*, 1991) and growth (e.g. Kingsolver & Woods, 1997). The relation between ectotherm physiology and temperature can be described by **thermal performance curves** (Huey & Stevenson, 1979, see Figure above). These curves are defined by a thermal optimum (i.e. temperature maximizing performance), critical thermal limits (i.e. $CTmin$ and $CTmax$ the lower and upper temperature allowing performance respectively) and a thermal tolerance (i.e. range of temperature allowing performance). Thermal performance curves determine the range of temperature at which a population or an individual can persist. For instance, Sinervo *et al.* (2010) predicted that climate change could lead to 39% of population extinction. They argue that, in absence of adaptation, body temperature should exceed upper thermal limit, leading to individual death, population extirpation and species extinction. However, thermal performance curves may evolve in response to the increase in temperature (Huey & Kingsolver, 1993; Angilletta *et al.*, 2002). Parameters of thermal performance curves vary among species, populations and individuals (Kealoha Freidenburg & Skelly, 2004; Sunday *et al.*, 2011; Artacho *et al.*, 2013). Natural selection could thus lead to evolutionary adaptation. The link between external temperature and body temperature could also be buffered by phenotypic, physiological and behavioral traits (Angilletta *et al.*, 2002). For example, behavioral thermoregulation allows individuals to cool themselves by hiding in shade areas, burrows and cooler microhabitats. Thermoregulation permits individuals to live into conditions where external temperature exceeds their thermal limits (Sunday *et al.*, 2014). Such traits could also change plastically or genetically in response to climate change. Moreover, multiple physiological and thermoregulatory traits often covary to form thermal types along a cold-hot continuum (Goulet *et al.*, 2017) that could also evolve to maintain optimal body temperature.

The Metatron

The Metatron (Figure 1.5) is an experimental system situated in the south of France (Ariège) composed of 48 interconnected semi-natural enclosures of 100 m^2 surface each (Legrand *et al.*, 2012). The enclosure size is equivalent to the common lizards' core home range size (Clobert *et al.*, 1994; Lecomte & Clobert, 1996; Boudjemadi *et al.*, 1999). Tarpaulins buried in the soil and nets prevent terrestrial and avian predation and lizard escapes. Each enclosure acts as a mini-ecosystem with vegetation, insect communities and habitat heterogeneity with rocks, wood logs for thermoregulation and small water ponds. Enclosures shelter 133 plant species (estimated in June 2018) and at least 82 invertebrate families (mostly arachnids and insects, estimated in 2017).

Enclosures can be connected through a 19 meters corridor, corresponding to the minimal dispersal distance of the common lizard (Clobert *et al.*, 1994, 2012). Corridors can be easily opened and closed to manipulate landscape connectivity. When corridors are open, lizards could disperse from one enclosure to another.

Temperature, hygrometry and illuminance are automatically recorded every 30 minutes in each enclosure and can be manipulated via the actuation of motorized shutters and a sprinkler system. For this experiment, we set up two climatic treatments, by closing the shutters at different temperatures. For the "present-day climate" treatment, the shutters automatically closed when ambient temperature in the enclosures reached 28°C. For the "warm climate" treatment, the shutters closed when ambient temperature reached 38°C. Given that enclosures are intrinsically warmer than outside, the present-day climate treatment allows to obtained thermal conditions similar to the mean temperature outside of the Metatron (temperature in the nearby meteorological station of Saint-Girons Antichan (Bestion *et al.*, 2015a,b)). During the three years of our experiment, the mean summer daily temperatures in the warm climate treatment were on average 1.5 degrees warmer than the present-day climate treatment. Over the three years of experiments, the mean summer temperature of the present-day climate treatment was 26.03±0.15°C and the one for the warm climate treatment was 27.42±0.18°C. As our treatments depend on outdoor climatic conditions, the treatments were efficient during the summer daytime (from mid -

Figure 1.5 – The metatron. a) is a aerial view of the system. b) is a view of an enclosure from outside. c,d,e,f) are views from inside of an enclosure, showing vegetation (c,f), wood logs (d) and water pond (e). We can see the entrance (closed) of a corridor in the background of picture (f)

June to mid - September) and the difference between treatments varied with the weather. The mean summer temperature could therefore be slightly different between the years (26.23±0.25 and 27.71±0.26 in 2015, 26.34±0.24 and 27.88±0.24 in 2016, 25.52±0.24 and 26.67±0.25 in 2017 for present-day climate treatment and warm climate treatment respectively). Relative to the 1986-2005 period, global mean surface temperature increase is predicted to be +1.5°C or more in 2046-2065 for scenario RCP4.5 and RCP8.5 and for

all scenarii in 2080-2100 except RCP2.6 (IPCC (2014), Table 1.1).

Experimental design and chronology of the experiment (Figures 1.6,1.7)

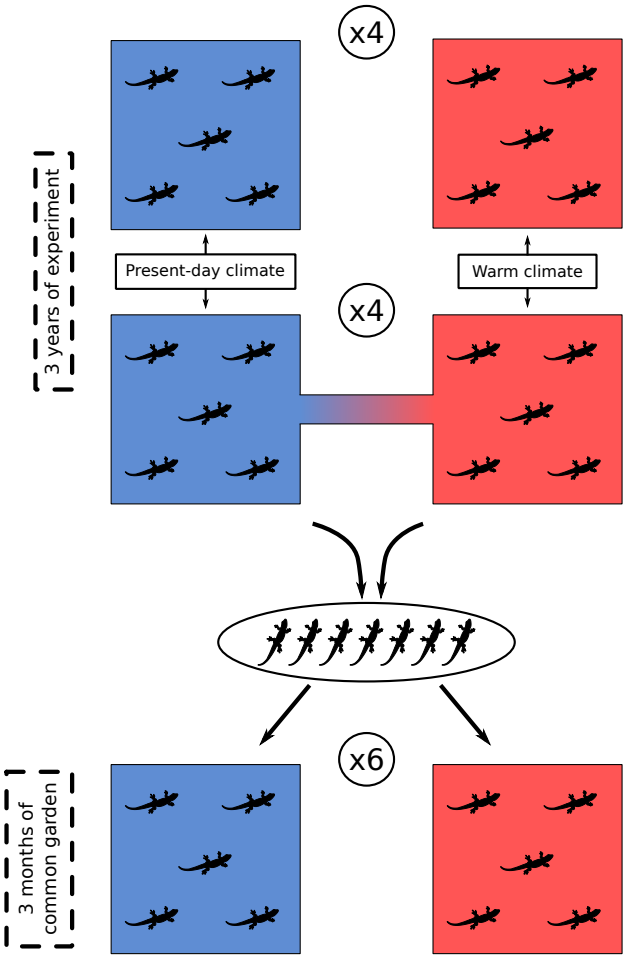


Figure 1.6 – Experimental design of the experiment performed in the Metatron. Pairs of isolated (4 pairs) and connected (4 pairs) enclosures (with one present-day (blue) and one warm (red) climate) were built. Populations of lizards were introduced and lived there for 3 years. We then performed a reciprocal common garden experiment into 12 enclosures, 6 with present-day climate (blue) and 6 with warm climate (red). The individuals were split between the two treatments of the common garden (see details in Chapter 3). The reciprocal common garden lasted three months

Our experimental design consisted in 16 enclosures with two climatic and two connectivity treatments (Figure 1.6). Populations of lizards were maintained in the system for three years. At the end of these three years of treatments, we did a reciprocal common garden experiment to test whether the changes in phenotypes resulted in differences in individuals' success in the different climatic conditions. Compared to a classic common garden, where all the individuals are raised in the same condition, we distributed

the individuals in the two climatic conditions. We used 12 isolated enclosures, 6 with a present-day climate treatment and 6 with a future warm climate treatment. The reciprocal common garden lasted 2.5 months, from July to mid September 2018. Because of the short period of time, and because we did not measure phenotypes at the end of the reciprocal common garden, we did not use it to distinguish between evolutionary and plastic processes that could occur during the three years of experiment. The chronology of the experiment is described in Figure 1.7. More details about experimental design and chronology are provided in Chapters 2 and 3.

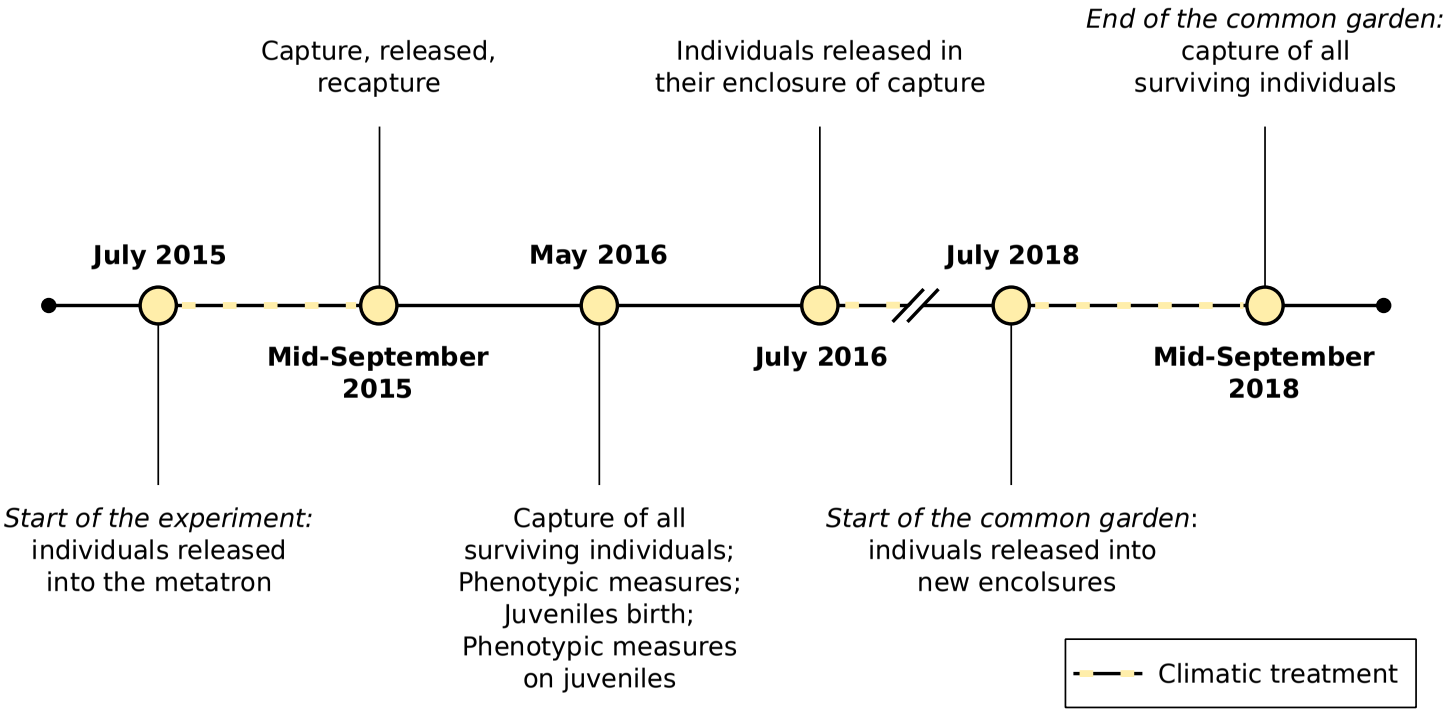


Figure 1.7 – Chronology of the experiment

5.2 The modeling approach

I used an individual based model (IBM) to test how different dispersal strategies (matching habitat choice versus random dispersal) modify predictions of species persistence under climate change compared to model where random dispersal was included (Chapter 4). IBMs are stochastic models allowing to model explicit landscape and species. Compare to analytical and deterministic models, complex processes and mechanisms could be integrated. However, conclusions could be strongly dependent on the initial conditions and parameter values, requiring to replicate simulations and to explore a wide range of parameters.

We modeled a two dimensional, continuous landscape on which a climatic gradient occurred on the latitudinal axis. We simulated two levels of climate change by increasing through time the temperature at each latitude (1°C per 100 years or 2°C per 100 years). On this landscape, individuals of a virtual species were distributed. The life cycle of this species is described in Figure 1.8. We modeled a sexual species with two age stages (juveniles and adults). Individuals could disperse (either randomly or following matching habitat choice), reproduce (for adults only) and then survived or died. Details about life cycle, survival rules, reproduction and dispersal decisions are provided in Chapter 4.

With this model, we ran simulations with matching habitat choice and simulations with random dispersal. We followed populations' genetic composition through space and time. After quantifying the adaptiveness of gene flow under both dispersal modes, we evaluated the influence of matching habitat choice on (i) extinction risk at the edges of and within the spatial range, (ii) on the proportion of the geographical range within which the species goes extinct during climate change and (iii) on the time to species extinction.

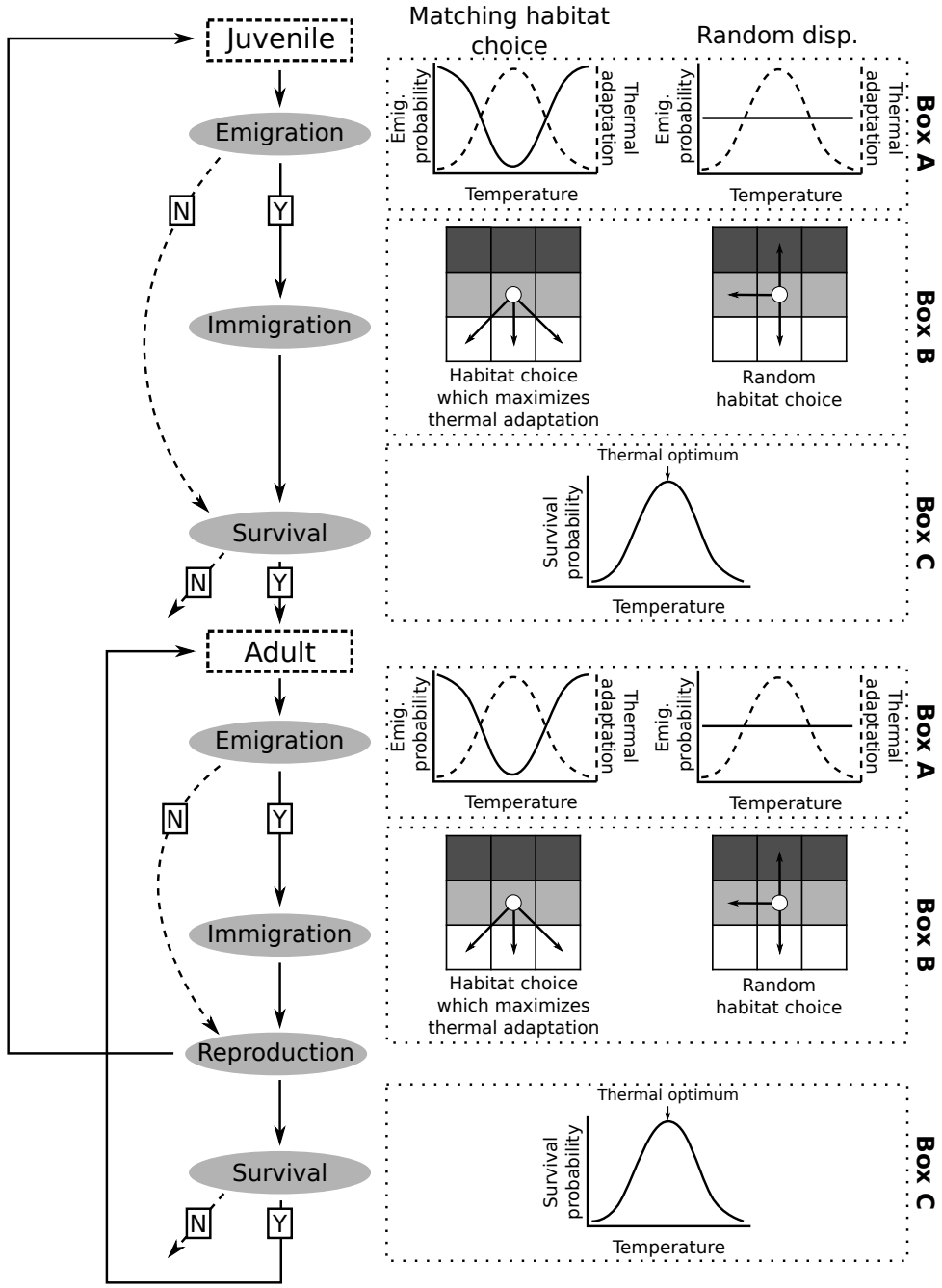


Figure 1.8 – Flow diagram of the model. The left side of this diagram depicts the life cycle of the modeled species. At birth, a juvenile could disperse (emigration and immigration), then survive to become an adult or die. As an adult, it could disperse again (emigration and immigration), reproduce and survive or die. The adult stage lasted until the individual died. The right side shows how we modeled the different events of the life cycle (i.e. emigration, immigration, survival) in the matching habitat choice and random dispersal modes. For both modes, survival was a Gaussian function of local temperature (Box C) and so was thermal adaptation (dashed line, Box A). Emigration probability (solid line, Box A) depended on local temperature in the matching habitat choice mode and was constant in the random dispersal mode. After leaving its habitat, an emigrant with a given phenotype (i.e. the color of the circle) settled in a matching habitat choice its phenotype (i.e. same color) for the matching habitat choice mode while it settled in a randomly chosen habitat when dispersal was random (Box B).

2 Connectivity among habitats buffers climate change effects on population dynamics

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1 Abstract

Contemporary climate change affects population dynamics through changes in life-history traits (i.e. survival, growth, reproduction and dispersal). Changes in population dynamics encompass changes in age structure, in individual mean body size and in density. However, landscape structure could modulate effects of climate change on population dynamics by affecting movements among populations. Dispersal could indeed allow individuals to use cool microclimates within a landscape as refuges to avoid overheating. Connectivity among habitats may therefore buffer the influence of climate change on population dynamics. Here, we experimentally investigated the impacts of warmer climates on population dynamics (density, age structure and size structure) in landscapes varying for their habitat connectivity. We monitored for three years populations of the common lizards (*Zootoca vivipara*) living in experimental enclosures where climatic conditions and connectivity were simultaneously manipulated. We found that the influence of warmer climate on population dynamics depended on landscape structure. In isolated populations, warmer climate led to a faster pace-of-life compared to present-day climate, with increased growth and earlier reproductive onset, and lowered survival of older individuals. The multiple impacts of climate change on life-history led to (i) a modification in population age structure towards younger individuals,(ii) an increase of individual body size but (iii) no effects on population density. However, when populations inhabiting different microclimates were connected, there was a striking change in the observed impacts of climatic conditions on population dynamics. Indeed, we found that populations in connected treatments displayed no differences in age structure, while density in cooler microclimate became lower than density in warmer microclimate. These differences may be due to the differences in dispersal between climates, where there was an uneven flow of dispersers and differences in their phenotypic traits between warmer and cooler climatic conditions. Our results highlighted the importance of considering landscape structure when studying the influence of climate change on population dynamics. Furthermore, as ecological and evolutionary processes are closely related (i.e. eco-evolutionary dynamics), the influence

of landscape structure on population dynamics could affect population adaptation and its role in population persistence under climate change.

2 Introduction

Contemporary climate change is a major threat to biodiversity worldwide (Parmesan, 2006; Urban, 2015; Selwood *et al.*, 2015). Climate warming can result in local population extirpation (Sinervo *et al.*, 2010), changes in populations' spatial distribution (i.e. range shift, Parmesan *et al.*, 1999; Chen *et al.*, 2011), phenotypic composition (Charmantier *et al.*, 2008; Boutin & Lane, 2014) and dynamics (Whitfield *et al.*, 2007; Ozgul *et al.*, 2010; Bestion *et al.*, 2015b). Climate-dependent population dynamics have been studied in different taxonomic groups (e.g. insects (Deutsch *et al.*, 2008), birds (Jenouvrier *et al.*, 2018), mammals (Ozgul *et al.*, 2010), reptiles (Le Galliard *et al.*, 2010)) and encompass changes in population density, age and size structure (Whitfield *et al.*, 2007; Daufresne *et al.*, 2009; Cunningham *et al.*, 2017). For instance, climate change affects population size structure and/or age structure in ectotherms (Daufresne *et al.*, 2009; Gardner *et al.*, 2011; Sheridan & Bickford, 2011). These alterations of population dynamics result from changes in individuals' life-history traits, namely survival, growth, reproduction and dispersal. In fish populations, climate change positively affects body growth and survival of small individuals while it has negative effects on the survival of bigger individuals, affecting populations size structure (Vindenes *et al.*, 2014). These changes in population dynamics could result in changes in community composition (Brose *et al.*, 2012). Such climatic impacts on population dynamics are therefore central to predict the future of biodiversity under climate change.

However, climatic impacts are often studied independently of other contemporary environmental changes simultaneously acting on population dynamics. For instance, landscape fragmentation is another major anthropogenic threat likely interacting with climate change (Opdam & Wascher, 2004; Brook *et al.*, 2008). Landscape fragmentation splits suitable habitats into a number of small and isolated patches (Fahrig, 2003). As a consequence, landscape fragmentation alters population dynamics by reducing habitat size, increasing impacts of demographic/environmental stochasticity and limiting individual movements (i.e. dispersal) among populations. Dispersal is a cornerstone of popula-

tion dynamics via the direct effects of emigration and immigration rates on population density (Burgess & Marshall, 2011). Furthermore, dispersers often have particular life history traits (i.e. dispersal syndrome, Clobert *et al.*, 2009; Ronce & Clobert, 2012; Cote *et al.*, 2017) which may affect the dynamics of populations at emigration and immigration (Bowler & Benton, 2005; Burgess & Marshall, 2011; Sih *et al.*, 2012). Landscape fragmentation may therefore modulate population dynamics by (i) limiting the number of emigrants and/or immigrants (Lecomte *et al.*, 2004; Fahrig, 2003), (ii) preventing individuals with particular characteristics from dispersing (Boudjemadi *et al.*, 1999; Barnes *et al.*, 2015) and (iii) decreasing survival rate through increased dispersal costs (Johannesen *et al.*, 2000; Bonte *et al.*, 2012; Fahrig, 2003).

Due to their respective effects on life-history traits, climate change and landscape fragmentation may interact in multiple ways to drive population dynamics. For example, detrimental impacts of climate warming on local population dynamics, through changes in reproductive onset, growth and survival rates, may be offset by individual movements into cooler microclimates. At the regional scale, the landscape is indeed composed of various microclimates where climate warming is not homogeneous (Ashcroft *et al.*, 2009). Habitats less affected by climate warming may play the role of climatic refuges (Pearson, 2006), preventing individuals to suffer from extreme conditions (Scheffers *et al.*, 2014; Suggitt *et al.*, 2018). Less affected habitats may also act as source populations allowing the rescue of (nearly) extinct populations. Fragmentation may prevent individuals to access such refuges, strengthening the climatic impacts on populations. In contrast, dispersal may also exacerbate the impact of climate change on population dynamics, if life-history traits of immigrants correspond to life-history traits favored under climate change. In that case, high connectivity may promote difference in population dynamics between microclimates and reinforce climate change effect on population dynamics.

Here, we experimentally investigated the impacts of warmer climates on populations' dynamics (density, age structure and size structure) in habitats varying in their connectivity. We monitored populations of the common lizard (*Zootoca vivipara*) for three years in an experimental system where both climatic conditions and connectivity were

simultaneously manipulated. Previous studies showed that both climatic conditions and habitat connectivity influenced the dynamics of common lizard populations (Boudjemadi *et al.*, 1999; Sorci & Clobert, 1999; Lecomte *et al.*, 2004; Chamaillé-Jammes *et al.*, 2006; Marquis *et al.*, 2008; Le Galliard *et al.*, 2010; Bleu *et al.*, 2013; Bestion *et al.*, 2015b; Rutschmann *et al.*, 2016). Warmer climates had a positive effect on reproductive onset and success and on juveniles' body growth (Chamaillé-Jammes *et al.*, 2006; Le Galliard *et al.*, 2010; Bleu *et al.*, 2013; Bestion *et al.*, 2015b). However, these positive effects on early life stages were offset by higher mortality latter in life. This accelerated pace of life was predicted to decrease population growth rate and to lead to populations made of younger individuals (Bestion *et al.*, 2015b). However, connectivity between habitats may influence these climatic impacts on population dynamics. Cotto *et al.* (2015) recently showed that dispersing females have an accelerated pace of life compared to philopatric females. We therefore investigated if immigration of these particular individuals could accelerate pace of life in synergy with warm climatic conditions and reinforce climatic impacts on population dynamics, or if, conversely, climatic impacts were buffered by dispersal because it allowed to rescue populations with a low growth rate and to prevent cost of warmer climates e.g., through the use of microclimates and refuge areas.

3 Materials and methods

3.1 Model species

The common lizard (*Zootoca vivipara*) is a small viviparous lacertid (adult snout-vent length = 50-70 mm) widespread across Eurasia where it inhabits peat bogs and heathland. The average lifespan of this species is five years (Sorci & Clobert, 1999). Three age stages can be distinguished: juvenile (<1 year), yearlings (1 to 2 years) and adults (>2 years). Reproduction is mainly made by adults (Massot *et al.*, 1992), even if some yearlings also reproduce depending on their body size (Bestion *et al.*, 2015b). The common lizard has been studied as a model ectotherm species for more than 20 years (Massot *et al.*, 1992; Cote & Clobert, 2007b; Le Galliard *et al.*, 2008), particularly to study

the impact of contemporary climate change on population dynamics (Sorci & Clobert, 1999; Chamaillé-Jammes *et al.*, 2006; Marquis *et al.*, 2008; Le Galliard *et al.*, 2010; Bleu *et al.*, 2013; Bestion *et al.*, 2015b; Rutschmann *et al.*, 2016). The individuals used in this study were descendants of lizards captured in the Cevennes, France, in 2010 (Licence no. $2010-189-16$ DREAL). Lizard populations were maintained in the Metatron (see next section) for several experiments (Bestion *et al.*, 2015a,b, 2017) and intermixed regularly to prevent high levels of inbreeding. In our study system (Ariège, France), lizards hibernate from November to February and mate just after emergence. Females lay around 5 (1-12) soft-shelled eggs (Massot *et al.*, 1992). Parturition starts in June and all parturition occurred in a period of one month on average. Juveniles emerge from the eggs within one hour after parturition and are immediately independent (Massot *et al.*, 1992).

3.2 Experimental design

We used the Metatron, an experimental system located in the South of France (Ariège) and composed of 48 interconnected semi-natural enclosures of 100 m^2 each (Legrand *et al.*, 2012). Tarpaulins buried in the soil and nets prevent terrestrial and avian predation and lizard escape. Each enclosure acts as a mini-ecosystem with vegetation, invertebrate communities and habitat heterogeneity with rocks, wood logs and small water ponds. Enclosures can be connected through a 19 meter corridor, corresponding to the minimal dispersal distance of the common lizard (Clobert *et al.*, 1994). Temperature, realtive humidity and illuminance are automatically recorded every 30 minutes. Temperature can be manipulated via motorized shutters and each enclosure can be watered through sprinklers. In 2012, we developed two climatic treatments by closing the automatic shutters at different temperature (Bestion *et al.*, 2015b). For the "present-day climate" treatment, the shutters automatically closed when ambient temperature in the enclosures reached 28°C. For the "warm climate" treatment, the shutters closed when ambient temperature reached 38°C. Given that enclosures are intrinsically warmer than outside, the present-day climate treatment results in thermal conditions similar to the mean temperature outside of the Metatron (temperature in the nearby meteorological station of Saint-Girons An-

tichan (Bestion *et al.*, 2015b)). The mean summer daily temperatures in the warm climate treatment were on average 1.5 degrees warmer than the present-day climate treatment (see General introduction for more details). As our treatments depended on outdoor climatic conditions, the treatments were efficient during the summer daytime (mid-June – mid September) and the difference between treatments varied with the weather. Relative to the 1986-2005 period, global mean surface temperature increase is predicted to be +1.5°C or more by 2046-2065 for scenario RCP4.5 and RCP8.5 and for all scenarii in 2080-2100 except RCP2.6 (IPCC (2014)).

Our experimental design consisted in 16 enclosures with two climatic and two connectivity treatments. Eight pairs of enclosures, one with a present-day climate and one with a warm climate, were created. The corridor between the two enclosures was open for four pairs allowing lizards to move from one climatic treatment to the other (i.e. connected treatment) while the corridor was closed for the four remaining pairs preventing any movement (i.e. isolated treatment). It allowed us to test how the influence of warmer climatic conditions on population dynamics was affected by connectivity between micro-habitats. In the connected treatments, corridors were opened from March to mid-October spanning the entire period of lizards' activity. In 2017, we opened corridors by the end of March due to the maintenance of the system. However, it should not have much influence on the impacts of connectivity as it covers a small period of time.

The experiment started in 2015 and spanned 3 years. Early July 2015, 546 lizards (240 adults and 306 juveniles) were released into the 16 enclosures. Populations in each enclosure were composed of 10 females, 5 males and 19 $\pm$ 1 juveniles, corresponding to intermediate density observed in natural populations and used in other semi-natural systems (Massot *et al.*, 1992; Cote & Clobert, 2007a). All individuals were of known age because they inhabited the Metatron since birth. We also split clutches among different enclosures to enhance genetic diversity within populations and released juvenile in enclosures without their mother to avoid kin competition (Cote *et al.*, 2007). All the lizards present in the system were individually identified (tagged by toe clipping) and measured for body size (i.e. snout-vent length) and a tail tip was taken for genetic identification

and paternity analyses. We ensured that there was no difference in age structure and body size between treatments ($p > 0.55$ for all comparisons).

3.3 Population monitoring

From 2016 to 2018, we applied the same protocol to monitor populations. In May, before females started laying eggs, all the individuals were recaptured from enclosures and brought back to the laboratory. They were identified, measured for body size and maintained in individual terraria (17x34x20 cm for adult females and gravid yearling females and 11x17x15 cm for males and non-gravid yearling females). Terraria contained a 3 cm sterilized litter layer, a petri dish with water, a piece of absorbent paper, a cardboard and a plastic tube as a shelter. A light bulb (25 W) and an ultraviolet lamp (Zoomed Reptisun 5.0 UVB 36 W) provided heat for thermoregulation and light 6 h per day (from 9:00 to 12:00 and from 14:00 to 17:00). Lizards were lightly sprayed with water three times a day (in the morning, at mid-day, and in the evening) and offered two crickets (*Acheta domestica*) daily. Females laid eggs in their terrarium and the juveniles were isolated from their mother directly after parturition. They were measured, weighted, marked and a tail tip was taken for genetic sampling. From these captures, we could further identify individuals which dispersed between connected enclosures.

Early July, all males, females and their clutch were released into the Metatron. We released adult individuals back to the enclosure they were captured from in May, and juvenile individuals in the same enclosure as their mother. Over the course of the experiment, three populations went extinct (two in 2016 and one in 2017). In 2016, the two extinct populations (one of each climatic treatment in isolated treatment) were reinitialized with the same density, age-structure and sex-ratio as in 2015 using lizards from other experiments. In 2017, the extinct population (from present-day climate in isolated treatment) was not reinitialized because of the lack of available lizards with same age and sex as in 2015.

3.4 Statistical analysis

Statistical analyses were performed in two steps. First, we explored the additive and interactive effects of climate and habitat connectivity on population density, age structure and size structure. Second, we analyzed each life-history trait separately to investigate processes underpinning changes in population dynamics.

Population density, age structure and size structure

We used generalized mixed model with Poisson distribution to test for the influence of climatic and connectivity treatments on population density and the age of individuals composing populations. We used linear mixed models to test for the influence of climatic and connectivity treatments on the size of individuals composing populations. Fixed effects were climatic treatment, connectivity treatment and their interaction. For population density, the model included climatic treatment, connectivity treatment, number of years since population initialization (hereafter referred to as "time"), and their interactions. Only the linear effect of time was considered due to the low number of levels for this variable. When populations were reinitialized after extinction, the time had 0 as a value. We only used data after at least one year of treatments and therefore exclude the data at time 0 from the analyses. For population age structure and population size structure, the model was run at the individual level with individual age and individual body size as dependent variables respectively. Independent variables included climatic treatment, connectivity treatment, time, and their interactions. Independent variables also included sex and population density. Density was included in the models to account for the per capita influence of each individual in the age structure and size structure of its population (i.e. at low density, the relative contribution of each individual in the structure of its population is greater than at high density). In a second model, age of the individuals was also included in size structure analysis to disentangle the direct effect of climate on body size from its indirect effect though its influence on age (Table S2.3). In all models, the population identity was modeled as a random intercept to account for the dependency of individuals of same population. For models studying population den-

sity, the population identity was included as random intercept to take into account the repeated model structure. To investigate further the interaction between treatments, the effect of climatic treatments was analyzed in connected and isolated populations separately. Models included climatic treatment, time, their interaction and sex as fixed effects and population identity as random effect.

Life-history traits

All individuals older than 1-year old were considered as adults and analyzed together, while younger individuals (i.e. juveniles) were analyzed separately. We analyzed in adults and juveniles the females' probability of gravidity, the clutch size of (gravid and non-gravid) females, the survival probability over the past year and the body growth over the past year from every experimental year (2016, 2017 and 2018, hereafter named t1, t2, and t3). In the connected treatment, the dispersal status of juveniles and adults (i.e. disperser or resident) was also analyzed. Dispersal status of individuals was determined by comparing the population where they were released to the one where they were recaptured the year after. Individuals that moved from a population to the another after one year were considered dispersers, whereas others were considered as residents. We used generalized mixed models with binomial distribution for the probabilities of gravidity, survival and dispersal, with zero-inflated Poisson distribution for clutch sizes and a linear mixed model for body growth. All models included climatic treatments, connectivity treatments, time, and all their possible two-way and three-way interactions. Models including the three-way interaction did not converge for juveniles reproductive traits (i.e. the probability of gravidity and clutch size) due to a low number of gravid juveniles and for the adults' probability of gravidity. Triple interactions were thus excluded from these particular analyses. Models further included covariates known to influence life-history traits: body size for all analyses, sex for survival and body growth analyses, and birth date in Julian days in the analyses of juveniles. Random intercepts included enclosure identity, individual ID for analyses in which the same individual could be present more than once, and family identity for analyses on juveniles as sibs from the same clutch were not independent.

To investigate interactions between climatic and connectivity treatments, we further ran these analyses in isolated and connected populations separately. Model structures were the same as described above without the connectivity treatment.

In connected populations, we also analyze dispersal probability to investigate whether dispersal patterns could explain differences in population dynamics. We added to the model structure described above the interaction between body size and climatic treatments because it can strongly influence dispersal decisions as well dispersal costs and benefits (Cote *et al.*, 2007).

Model selection procedure:

Model selection was performed using the following procedure. Full models with all fixed variables and random effects were built and random structure of each model was selected by AIC, following Zuur *et al.* (2009). Random structure minimizing AIC was then selected with the exception of enclosure identity which was kept in models because individuals are largely influenced by environmental conditions and because we were interested in population dynamics. All possible models with fixed effects were built and ranked by AIC and conditional estimates, standard errors, z-value, relative importance and p-value of all variables present in best models within a delta AIC of 2 were obtained through model averaging procedure (Burnham *et al.*, 2011). All analyses were performed using R software version 3.4.3 (http://cran.r-project.org/, R Core Team (2017)) with lme4, glmAMBD (for models using a zero-inflated poisson distribution) and MuMin packages.

4 Results

4.1 Effects of climate and connectivity on population structure

Population structure was altered by our 3 year manipulation of climatic conditions and of the connectivity among habitats. Population density depended on climatic conditions and habitat connectivity (Table 2.1, Figure 2.1a). Population density decreased through time in connected habitats only (Table 2.1, Figure 2.1a). Warmer conditions had a positive

influence on population density (Table 2.1, Figure 2.1a). This effect was mainly observed in connected habitats (Table S2.1, S2.2, Figure 2.1a,) even if the interaction between connectivity and climatic conditions was not retained in the best models.

Climatic conditions differentially influenced population age structure in isolated and connected habitats (Table 2.1, Figure 2.1b). When isolated,age structure of a population was biased towards younger individuals in warmer conditions (Table S2.1) while climatic conditions had no influence on mean population age in connected populations (Table S2.2).

Finally, population body size structure depended on the three way interaction between climatic conditions, connectivity and time (Table 2.1, Figure 2.1c). In connected populations, there was a difference in individuals' body size appearing through time with larger individuals in warm than in present-day climates (Table S2.2, Figure 2.1c). Climatic conditions had no influence on individuals' body size in isolated populations even if there was an overall decrease in body size through time (Table S2.1, Figure 2.1c). However, when we controlled by individual's age in the analysis, both connected and isolated populations were composed of bigger individuals in warm than in present-day conditions and this effect increased though time (Table S2.3, Figure S2.1).

4.2 Effects of climate and connectivity on life-history traits

We then studied differences in life-history traits to explain observed changes in population structure. Climatic conditions differently influenced juveniles' reproduction in connected and isolated populations (Table 2.2, Figure 2.2a). Warmer conditions increased the reproductive output of juveniles in isolated population, but not in connected populations. One-year old juveniles had overall larger clutches in warmer conditions, due to their higher probability of gravidity in isolated populations only (Table 2.2, Table S2.4, S2.5, S2.6, Figure S2.2a). There was no influence of climatic conditions on adult reproductive success (Table 2.2, Table S2.6, Figure 2.2b, Figure S2.2b), while connectivity had a positive effect on adult reproductive output, increasing over time.

Juvenile body growth was also positively influence by warm conditions (Table S2.6, Figure S2.2c). Population isolation had a negative influence on juvenile growth rate (Ta-

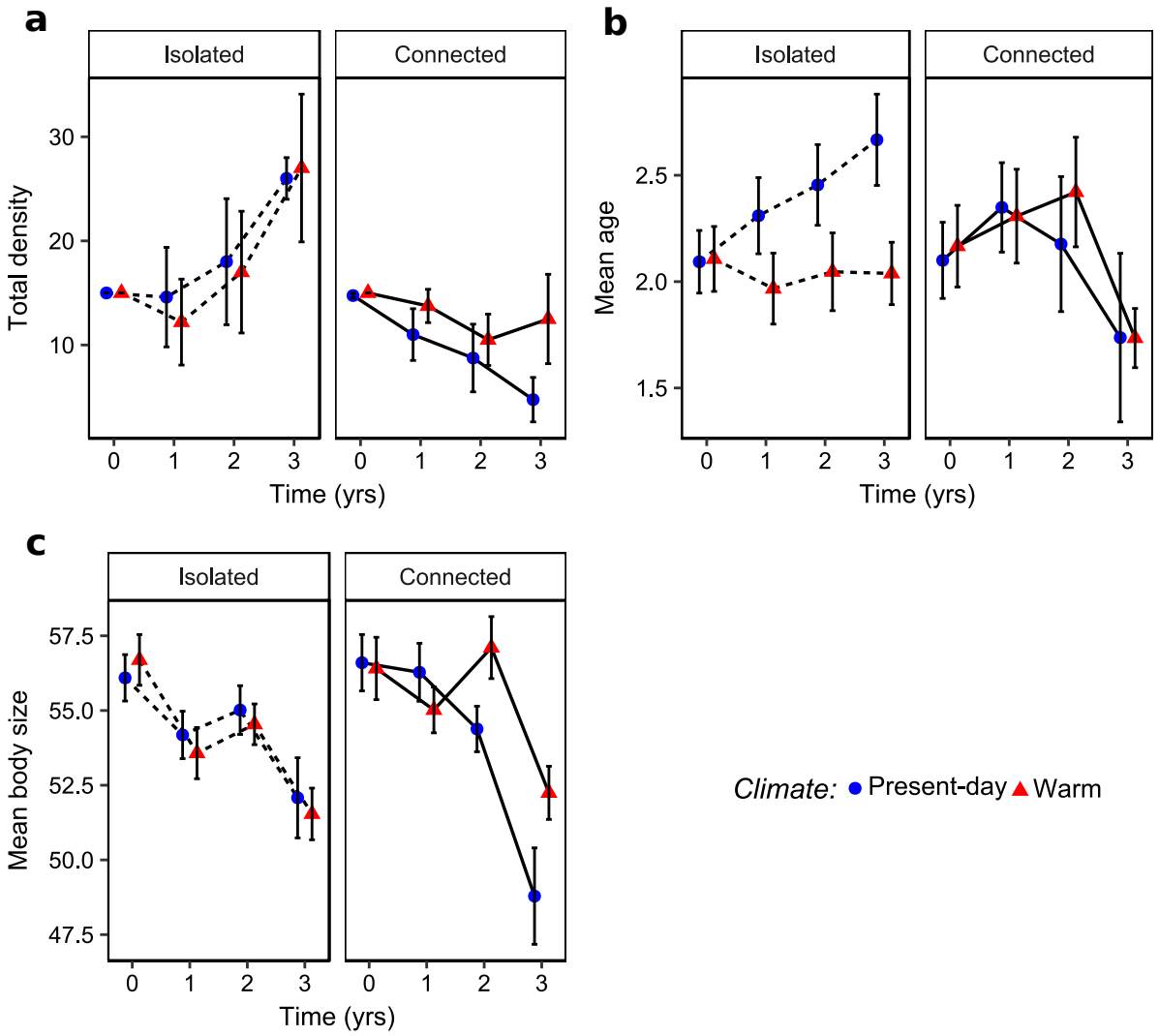

Figure 2.1 – Population dynamics: Total density (a), mean age (b) and mean body size (c) of populations through time in isolated (dashed lines) and connected (solid lines) habitats under present-day (blue circles) and warm climate (red triangles). Mean ± SE are represented

ble S2.6) but it magnifies the climatic impacts on growth rate (Tables S2.4, S2.5). Climatic conditions and connectivity had a weak influence on adult growth rate (Table S2.6, Figure S2.2d).

Finally, warmer conditions had a positive but weak effect on juvenile survival probability (Table 2.2, Figure 2.2c). This effect mainly appeared in isolated populations (Figure 2.2c) even if the interaction between climatic condition and connectivity was not retained in best models (Tables S2.4, S2.5). Climatic conditions also influenced adult survival probability, but this effect varied with time and habitat connectivity to a lower

	Estimate	SE	z-value	RI	P-value
Population density					
Intercept	2.34	0.28	8.01	1	<0.001
Climate	0.21	0.34	0.59	0.59	0.557
Connectivity	-0.14	0.35	0.38	1	0.702
Time	0.05	0.08	0.6	1	0.545
Time*Climate	0.2	0.08	2.34	0.59	0.019
Time*Connectivity	-0.27	0.08	3.16	1	0.002
Age structure					
Intercept	0.86	0.06	15.37	1	<0.001
Climate	-0.21	0.07	3.11	1	0.002
Connectivity	-0.22	0.1	2.16	1	0.031
Time	0.05	0.04	1.27	1	0.203
Density	-0.06	0.04	1.64	0.58	0.102
Sex	0.12	0.05	2.29	1	0.022
Climate*Connectivity	0.24	0.11	2.12	1	0.034
Time*Connectivity	-0.17	0.06	2.78	1	0.005
Body size structure					
Intercept	0.16	0.12	1.41	1	0.159
Climate	-0.13	0.15	0.86	0.66	0.389
Connectivity	-0.07	0.2	0.37	1	0.712
Time	0.21	0.05	4.38	1	<0.001
Density	-0.14	0.05	2.82	1	0.005
Sex	-0.59	0.09	6.35	1	<0.001
Climate*Connectivity	0.37	0.22	1.67	0.66	0.095
Time*Climate	0.04	0.07	0.51	0.66	0.607
Time*Connectivity	-0.33	0.14	2.36	1	0.018
Time*Climate*Connectivity	0.28	0.13	2.08	0.66	0.038

Table 2.1 – Population dynamics. All models included population identity as random intercept

extent (Table 2.2, Figure 2.2d). In isolated populations, warmer conditions overall decreased adult survival probability and this effect disappeared over time (Table S2.7, Figure 2.2d). The same effect was observed in connected populations the first year, but adult survival was then better in warmer than in present-day climate (Table S2.5, Figure 2.2d). Connectivity also had a negative effect on adult and juvenile survival probability, but this effect varied over time in opposite ways for adults and juveniles (Table 2.2).

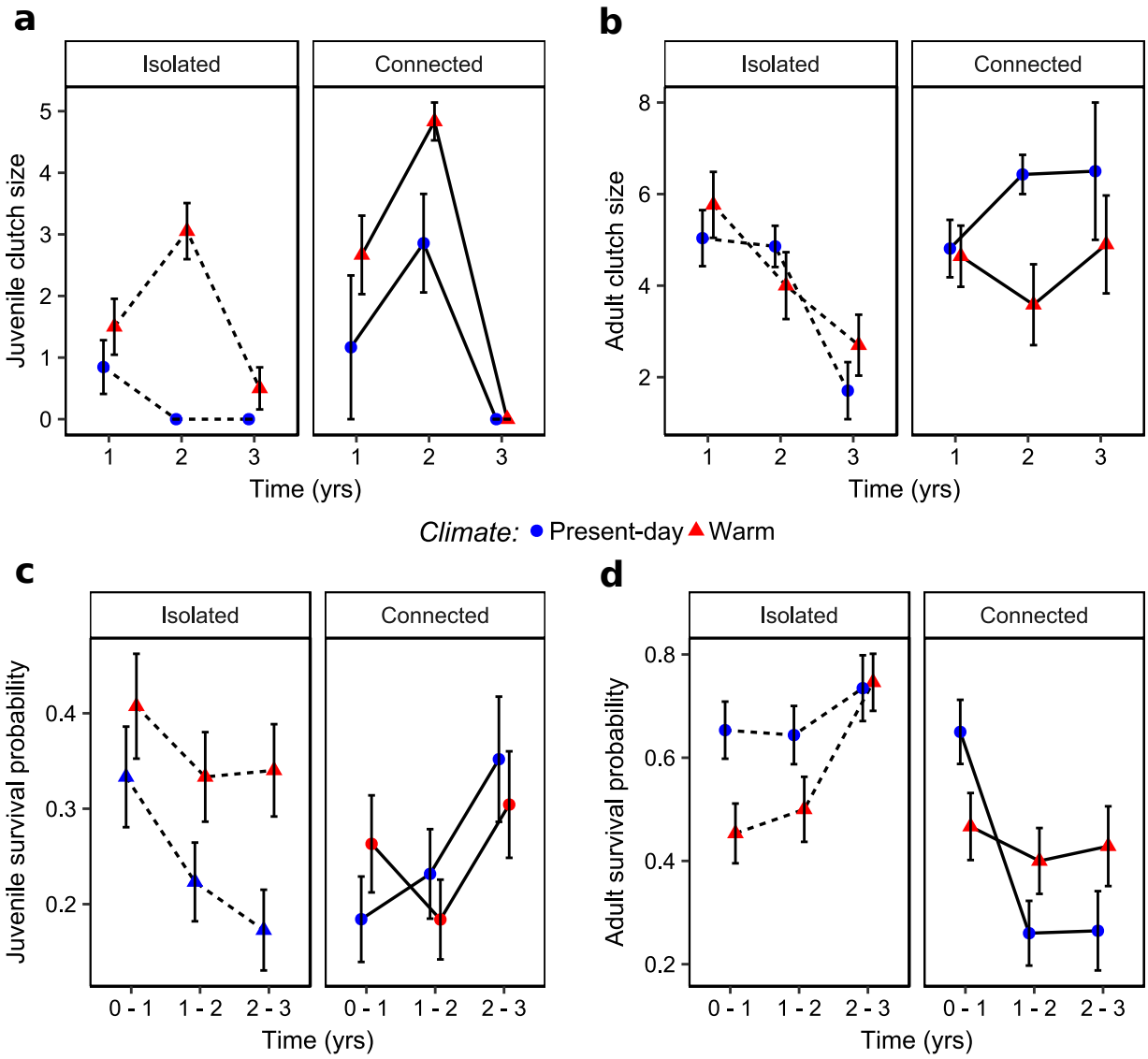

Figure 2.2 – Life history traits: Juvenile clutch size (a), adult clutch size (b), juvenile survival probability (c) and adult survival probability (d) through time in isolated (dashed lines) and connected (solid lines) habitats under present-day (blue circles) and warm climate (red triangles). Mean ± SE are represented

4.3 Effects of climate on dispersal

In connected populations, adult individuals were more likely to disperse from present-day than from warm climate (Table 2.3, Figure 2.3b). However, these effects varied with body size. Adult dispersers from the present-day climate had smaller body size than residents of the present-day climate and dispersers from the warm climate had larger body size than residents of the warm climates (Table 2.3, Figure S2.3b). In juveniles, individuals were also more likely to disperse from present-day than from warm climate,

Variable	Estimate	SE	z-value	RI	P-value
Clutch size of juveniles					
Intercept	-0.65	0.47	1.38	1	0.169
Climate	1.64	0.57	2.85	1	0.004
Connectivity	1.53	0.5	3.01	1	0.003
Time	-0.81	0.38	2.11	0.67	0.0351
Climate*Connectivity	-1.39	0.48	2.85	1	0.004
Body size	0.47	0.2	2.38	0.84	0.017
Time*Climate	0.92	0.4	2.28	0.67	0.022
Time*Connectivity	0.16	0.26	0.6	0.14	0.548
Clutch size of adults					
Intercept	1.68	0.04	37.5	1	<0.001
Connectivity	0.03	0.08	0.45	0.67	0.650
Time	-0.13	0.06	2.15	1	0.031
Body size	0.16	0.04	4.12	1	<0.001
Time*Connectivity	0.19	0.08	2.37	0.67	0.017
Survival probability of juveniles					
Intercept	-1.27	0.31	4.03	1	<0.001
Climate	0.47	0.34	1.36	0.47	0.173
Connectivity	-0.18	0.37	0.48	1	0.631
Time	-0.21	0.15	1.37	1	0.172
Birth date	-0.03	0.1	0.33	0.11	0.741
Body size	0.25	0.12	2.14	1	0.033
Sex	0.11	0.17	0.65	0.24	0.517
Time*Climate	0.13	0.18	0.7	0.11	0.482
Time*Connectivity	0.49	0.18	2.7	1	0.007
Survival probability of adults					
Intercept	0.03	0.32	0.09	1	0.924
Climate	-0.18	0.39	0.45	1	0.652
Connectivity	-0.74	0.41	1.81	1	0.071
Time	-0.33	0.18	1.85	1	0.064
Body size	0.03	0.09	0.33	0.2 0.741	
Sex	0.75	0.18	4.19	1	<0.001
Climate*Connectivity	0.55	0.68	0.81	0.26	0.418
Time*Climate	0.72	0.19	3.82	1	<0.001
Time*Connectivity	-0.62	0.19	3.32	1	<0.001

Table 2.2 – Life-history traits: Effects of climatic conditions and connectivity treatments on clutch size and survival probability of juveniles and adults. All models included population identity as random intercept. Random structure for model analysing the survival probability of juvenile also included family identity

but the pattern was weak and not constant over time (RI=0.35, Table 2.3, Figure 2.3a). Moreover, there was no difference between residents and dispersers regarding body size (Table 2.3, Figure S2.3a).

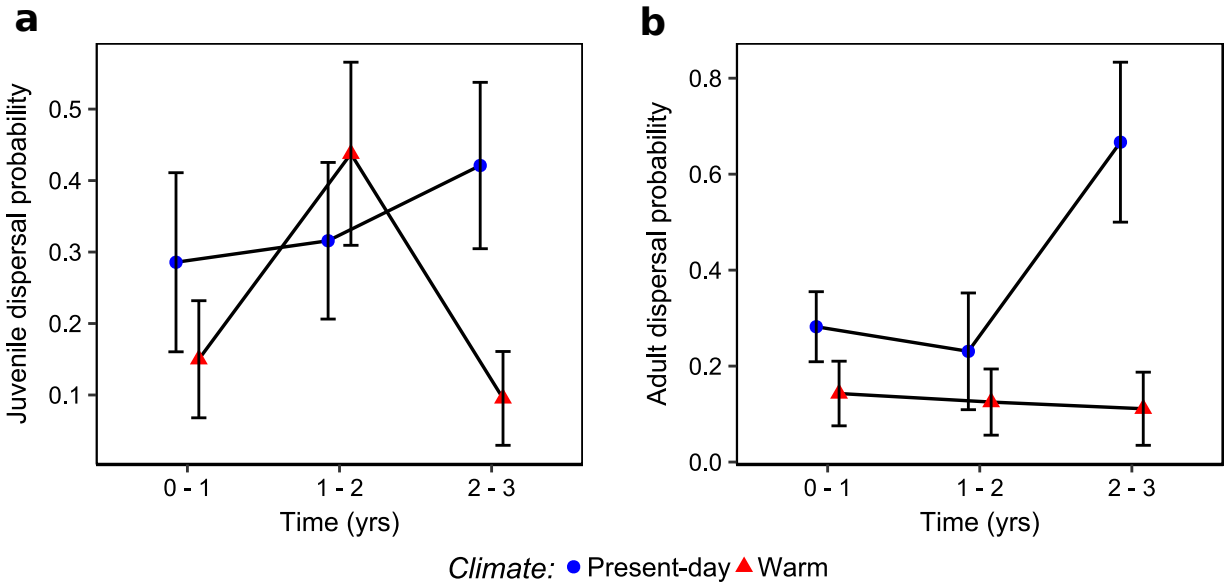

Figure 2.3 – Dispersal probability: Juvenile (a) and adult (b) dispersal probability through time under present-day (blue circles) and warm climate (red triangles). Mean ± SE are represented

Variable	Estimate	SE	z-value	RI	P-value
Juveniles' dispersal probability					
Intercept	-1.1	0.51	2.17	1	0.030
Sex	0.74	0.47	1.55	0.48	0.121
Climate	-0.73	0.64	1.14	0.35	0.254
Body size	-0.22	0.25	0.89	0.12	0.376
Adults' dispersal probability					
Intercept	-1.43	0.45	3.14	1	0.002
Body size	-0.85	0.39	2.16	1	0.031
Sex 1.08	0.52	2.07	1	0.039	
Climate	-1.57	0.6	2.59	1	0.010
Climate*Body size	2.32	0.64	3.56	1	<0.001
Time	0.13	0.24	0.51	0.27	0.610

Table 2.3 – Dispersal probability: effects of climatic conditions and body size on dispersal probability of juveniles and adults. All models included population identity as random intercept

5 Discussion

Our long-term warming experiment showed that when populations were isolated, climate change led to a faster pace-of-life, with increased growth and earlier reproductive onset, and lowered survival of older individuals. Further, and contrary to theoretical

expectations (Daufresne *et al.*, 2009; Gardner *et al.*, 2011; Sheridan & Bickford, 2011), individuals in warmer climate had bigger body sizes. The multiple impacts of climate change on life-history led to a modification in population age structure towards younger individuals but no effects on population density. However, our results depended on the configuration of the landscape. When we allowed populations in warm and present-day climate to be connected, there was a striking change in the observed impacts of climate change on population dynamics. Indeed, we found that populations in connected treatments displayed no differences in age structure, while density of present-day populations became lower than density of warm populations. These differences may be due to the differences in dispersal between climates, where there was an uneven flow of individuals and differences in phenotypic traits between warm and present-day climatic conditions.

In isolated populations, warmer climates led individuals to have a faster pace-of-life. Indeed, warmer conditions promoted body growth and reproduction of young individuals and decreased survival of adults. These results are consistent with those from Bestion *et al.* (2015b) showing the same pattern after one year of climatic treatments. We demonstrated that this accelerated pace-of-life was maintained over the three years of experiment. This maintained shift in life-history traits affected population age structure in such a way that the populations in warmer climates were composed of younger individuals than in present-day climate. Warmer climates further increased juvenile growth rate, likely through a faster metabolism (Gillooly *et al.*, 2001). As the access to reproduction is positively correlated to body size in this species (Cotto *et al.*, 2015), young individuals in warm climates had a higher reproductive success than in present-day climates. However, the effect of climatic conditions on juvenile reproductive outcome was not only due to its effect on body growth. The positive effect of warmer climate on clutch size was indeed still detected when controlling for individuals' body size, suggesting that warmer conditions influenced juveniles' reproduction not only through its effect on body growth rate. Warmer temperature could therefore select for individuals with faster pace of life (Brans & De Meester, 2018), increasing development rate, decreasing age and size at maturity, promoting reproductive success and reducing lifespan.

Change in population age structure was not associated with a change in population body size structure. Climate change commonly leads to a lowered body size, which has been advocated to be the third universal ecological response to climate change (Daufresne *et al.*, 2009; Gardner *et al.*, 2011; Sheridan & Bickford, 2011). This effect can come from both a decrease in size-at-age due to the faster metabolism at higher temperature (Temperature-Size rule) and from a change in population age structure (Daufresne *et al.*, 2009; Sheridan & Bickford, 2011). Our results are not consistent with this theory. We even found a positive effect of warmer climate on body size when controlling for age, because of the positive effect of warm climate on juvenile body growth . This pattern was general among studies on common lizards as a long term monitoring of their natural populations revealed a positive effect of climate change on individual body size (Chamaillé-Jammes *et al.*, 2006). One potential explanation for this discrepancy might come from the status of the common lizard as a generalist predator (Avery, 1966), as predators with a diverse diet could compensate their increased metabolic rate under climate change by shifting their diet towards bigger prey (Sheridan & Bickford, 2011).

We did not observe any influence of these climate-dependent life-history traits on the density of isolated populations. At a large scale, the effect of climate change on ectotherms density is predicted to depend on the geographic location, with populations of higher latitudes benefiting from warmer climates and those from low latitude decreasing in density (Deutsch *et al.*, 2008; Tewksbury *et al.*, 2008). In our study, the positive effect of warm climate on reproductive success of young individuals was offset by its negative effect on adult survival and therefore population density was not yet altered by climatic conditions. Bestion *et al.* (2015b), in a similar but shorter study, predicted population extirpation due to climate change in 20 years because of the higher sensitivity of population growth rate to adult survival than to yearling fecundity. We did not observe population decline in our three-year experiment. Adult survival rate even increased during the last year of experiment, suggesting that life-history traits may change over time. Longer experiments are needed to better understand and predict the future of populations under warmer conditions.

The impacts of climatic conditions on population dynamics and structure further vary with the connectivity among habitats. When individuals had access to a cooler microclimate, the effect of warm climate on population age structure was offset. This influence of habitat connectivity is explained by different impacts of climate on life-history than in isolated populations. In connected habitats, impacts on juvenile growth rate and survival were weaker compared to isolated populations and adult survival was even enhanced in warmer climates. In continuous landscapes, individuals can have access to warm and cool microclimates more easily and thus avoid temporary extreme climatic events (e.g. heatwaves (Scheffers *et al.*, 2014; Suggitt *et al.*, 2018)) and only make the most of the advantages of warmer environments without the costs. Intra annual movements between microclimates may limit the effect of warmer climatic conditions on population dynamics. In our study, we only recorded individual position once a year. Movements may therefore be underestimated and may quantify dispersal (i.e. individual movements between reproductive sites) rather than seasonal and daily movements to avoid overheating. Such movements could influence population dynamics through (i) emigration and immigration rates (Levins, 1969; Hanski & Gilpin, 1991; Burgess & Marshall, 2011) and (ii) the characteristics of dispersers (Burgess & Marshall, 2011; Clobert *et al.*, 2009; Jacob *et al.*, 2015a). We showed that both processes were involved in our results. First, we observed a strongly biased dispersal from present-day climate populations to warm climate populations. The flow of individuals affected the dynamics of populations in both climates, counterbalancing the influence of warm climate on population age structure and reducing population density in present-day climates. The biased dispersal was indeed stronger in adults than in juveniles (Table 2.3). This biased dispersal could have both decreased the density and the mean age in connected populations of present-day climates. We could have expected adults to disperse more from warm climate given the lower survival in warmer climates in isolated popualtions and the first year in connected populations (Figure 2.2d). However, 1.5°C warmer conditions may appear attractive and beneficial for an ectotherm species while the costs of living in may be less predictable for a candidate disperser (i.e. physiological exhaustion, heatwave). Second, we found that movements

were non-random regarding phenotypic traits. Adult immigrants from warm climate were larger than their resident counterparts, and conversely in present-day climates. Several hypotheses may explain this climate-dependent dispersal syndrome. Because metabolism and energetic needs depends on both temperature and body size (Gillooly *et al.*, 2001; Brown *et al.*, 2004), warmer conditions may bear additional costs for larger individuals, through enhanced energetic expenditure, stronger competition and rare resources, while being beneficial for the growth of smaller individuals. It might in turn drive dispersal decisions. Alternatively, body size may be related to thermal types. Ecotherms species may display a hot-cold continuum in phenotypic thermal adaptations (i.e. thermal types, Goulet *et al.* (2017)) which may be part of phenotypic and pace-of-life syndromes ranging from *r*- to *K*-types, including body size and potentially linked to habitat matching choice (Bestion *et al.*, 2015a). This dispersal syndrome was not found in juveniles. Given the small variation in juvenile natal size, it could explain the absence of syndrome regarding body size. Further experiments are needed to uncover the real explanations of these dispersal syndromes. Regardless of the explanations, our results show that the connectivity among microhabitats change the impacts of warmer climates on population dynamics.

Increasing efforts have been made in the last few decades to improve our understanding of climatic impacts on natural populations (e.g. Réale *et al.* (2003); Charmantier *et al.* (2008); Lepetz *et al.* (2009)) and to better predict their future (Thuiller *et al.*, 2005; Travis *et al.*, 2013; Bocedi *et al.*, 2013; Pellerin *et al.*, 2018). Only few studies tackled the combined effect of different drivers of global change on biodiversity (Warren *et al.*, 2001; Opdam & Wascher, 2004; Jetz *et al.*, 2007; Brook *et al.*, 2008; Hof *et al.*, 2011; Comte *et al.*, 2016). In this context, we demonstrated the complex interacting effect of climate change and habitat fragmentation on population dynamics. While climate change is not spatially homogeneous (Ashcroft *et al.*, 2009), maintenance of connectivity could buffer the impact of warm climatic conditions on population dynamics by allowing access to refuge areas (Scheffers *et al.*, 2014; Suggitt *et al.*, 2018). However, we showed that these movements between microclimates could be costly in terms of density for populations less affected by climate warming. Accounting for the central role of demography in local

adaptation and range shift (i.e. eco-evolutionnary dynamics, Schoener, 2011; Legrand *et al.*, 2017), landscape structure may shape population and species responses to climate change (Rutschmann *et al.*, 2016). Integrative studies taking into account climate change and landscape structure on population dynamics and its link to adaptation are therefore still needed to improve our understanding of anthropogenic actions on biodiversity.

6 Supplementary materials

Variable	Estimate	SE	z-value	RI	P-value
Population density					
Intercept	2.21	0.41	5.05	1	<0.001
Time	0.1	0.05	1.83	0.63	0.068
Age structure					
Intercept	0.82	0.07	12.23	1	<0.001
Time	0.09	0.04	2.12	1	0.034
Climate	-0.22	0.08	2.69	1	0.007
Density	-0.06	0.04	1.41	0.43	0.160
Sex	0.09	0.08	1.06	0.34	0.288
Time*Climate	-0.04	0.07	0.54	0.11	0.590
Body size structure					
Intercept	0.12	0.11	1.14	1	0.255
Climate	-0.13	0.13	0.99	0.36	0.321
Time	0.25	0.04	6.43	1	<0.001
Density	-0.14	0.05	2.99	1	0.003
Sex	-0.57	0.13	4.39	1	<0.001

Table S2.1 – Population dynamics in isolated populations: effect of climatic conditions on population density, population age structure and population mean age in isolated populations. All models included population identity as random intercept

Variable	Estimate	SE	z-value	RI	P-value
Population density					
Intercept	2.04	0.14	13.24	1	<0.001
Climate	0.44	0.19	2.17	1	0.030
Time	-0.27	0.13	2.04	1	0.042
Time*Climate	0.28	0.14	1.96	0.64	0.050
Age structure					
Intercept	0.67	0.07	9.17	1	<0.001
Time	-0.09	0.05	1.69	0.65	0.090
Density	-0.03	0.05	0.59	0.12	0.553
Sex	0.13	0.1	1.24	0.38	0.214
Body size structure					
Intercept	0.15	0.16	0.97	1	0.332
Climate	0.17	0.19	0.89	0.82	0.375
Time	-0.31	0.1	3.09	0.82	0.002
Time*Climate	0.32	0.12	2.66	0.82	0.008
Density	-0.09	0.06	1.38	0.37	0.169
Sex	-0.64	0.13	4.94	1	<0.001

Table S2.2 – Population dynamics in connected populations: effect of climatic conditions on population density, population age structure and population mean age in connected populations. All models included population identity as random intercept

Variable	Estimate	SE	z-value	RI	P-value
Body size structure					
Intercept	0.17	0.08	2.11	1	0.035
Climate	0.15	0.09	1.77	1	0.076
Connectivity	0.1	0.09	1.07	0.52	0.286
Time	-0.12	0.04	3.01	1	0.003
Age	0.68	0.03	21.78	1	<0.001
Density	-0.11	0.04	3.12	1	0.002
Sex	-0.69	0.07	10.32	1	<0.001
Time*Climate	0.11	0.05	2.24	1	0.025
Time*Connectivity	-0.06	0.05	1.03	0.19	0.304

Table S2.3 – Population body size structure: effect of climatic conditions and connectivity treatments on population body size structure when controlling by age. The model included population identity as random intercept

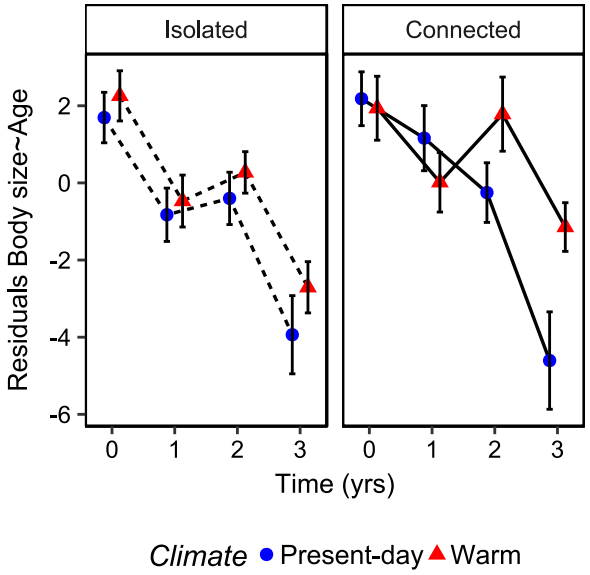

Figure S2.1 – Population body size structure: Residuals of body size $\sim$ age though time in isolated (dashed lines) and connected (solid lines) habitats under present-day (blue circles) and warm climate (red triangles). Mean $\pm$ SE are represented

Variable	Estimate	SE	z-value	RI	P-value
Juveniles' probability of gravidity					
Intercept	-2.64	0.84	3.1	1	0.002
Climate	1.55	0.74	2.08	1	0.038
Time	-0.29	0.41	0.7	0.3	0.485
Birth date	0.75	0.38	1.98	1	0.048
Body size	3.58	1.02	3.49	1	0.001
Clutch size of juveniles					
Intercept	-1.41	0.44	3.19	1	0.001
Climate	1.43	0.35	3.98	1	<0.001
Time	0.11	0.16	0.67	0.29	0.504
Body size	1.2	0.2	5.98	1	<0.001
Survival probability of juveniles					
Intercept	-1.62	0.56	2.91	1	0.004
Climate	0.93	0.75	1.24	0.63	0.214
Time	-0.43	0.25	1.72	0.66	0.085
Birth date	-0.19	0.13	1.4	0.24	0.162
Body size	0.41	0.15	2.75	1	0.006
Time*Climate	0.53	0.25	2.13	0.5	0.034
Juveniles' body growth					
Intercept	24.93	1.74	14.24	1	<0.001
Climate	3.9	2.03	1.91	0.86	0.056
Time	-3.97	0.88	4.52	1	<0.001
Birth date	-0.67	0.41	1.62	0.370	0.106
Body size	-2.53	0.52	4.85	1	<0.001
Sex	-2.13	0.66	3.22	1	0.001
Time*Climate	1.69	0.8	2.11	0.7	0.035

Table S2.4 – Life-history traits in isolated populations: Effects of climatic conditions on probability of gravidity, clutch size, survival probability and body growth of juveniles in isolated populations. All models included population identity as random intercept. Models analyzing juvenile probability of gravidity, survival and body growth also included family identity as random intercept

Variable	Estimate	SE	z-value	RI	P-value
Juveniles' probability of gravidity					
Intercept	-0.96	0.65	1.45	1	0.147
Climate	0.9	0.88	0.99	0.33	0.321
Birth date	0.93	0.46	1.97	1	0.048
Body size	2.46	0.72	3.34	1	<0.001
Adults' probability of gravidity					
Intercept	1.79	0.37	4.8	1	<0.001
Time	0.28	0.39	0.71	0.3	0.475
Body size	0.55	0.35	1.54	0.54	0.125
Clutch size of juveniles					
Intercept	1.44	0.16	8.87	1	<0.001
Body size	0.19	0.15	1.22	0.41	0.222
Clutch size of adults					
Intercept	1.75	0.07	24.81	1	<0.001
Climate	-0.08	0.11	0.67	0.28	0.504
Body size	0.14	0.06	2.29	1	0.022
Survival probability of juveniles					
Intercept	-1.51	0.26	5.78	1	<0.001
Climate	0.27	0.32	0.85	0.25	0.396
Time	0.14	0.15	0.89	0.26	0.372
Sexe	0.31	0.25	1.22	0.43	0.222
Survival probability of adults					
Intercept	-0.78	0.26	-3.03	1	0.002
Climate	0.16	0.30	0.53	1	0.595
Time	-0.94	0.21	-4.43	1	<0.001
Sex	0.79	0.26	3.00	1	0.003
Time*Climate	0.77	0.27	2.9	1	0.004
Juveniles' body growth					
Intercept	28.65	0.71	39.83	1	<0.001
Climate	0.75	0.93	0.79	0.3	0.429
Time	-1.78	0.47	3.76	1	<0.001
Body size	-1.75	0.5	3.44	1	0.001
Sex	-2.58	0.78	3.25	1	0.001
Adults' body growth					
Intercept	4.6	0.36	12.58	1	<0.001
Time	0.31	0.25	1.23	0.42	0.220
Body size	-3.56	0.26	13.41	1	<0.001
Sex	-3.96	0.52	7.48	1	<0.001

Table S2.5 – Life-history traits in connected populations: Effects of climatic conditions on probability of gravidity, clutch size, survival probability and body growth of juveniles and adults in connected populations. All models included population identity as random intercept. Model analyzing juvenile survival also included family identity as random intercept

Variable	Estimate	SE	z-value	RI	P-value
Juveniles' probability of gravidity					
Intercept	-2.13	0.54	3.95	1	<0.001
Climate	1.28	0.55	2.3	1	0.021
Connectivity	-0.56	0.54	1.02	0.29	0.306
Time	-0.18	0.32	0.57	0.2	0.571
Birth date	0.63	0.27	2.34	1	0.019
Body size	3.02	0.58	5.18	1	<0.001
Adults' probability of gravidity					
Intercept	1.58	0.29	5.49	1	<0.001
Connectivity	0.2	0.48	0.41	0.59	0.682
Time	-0.73	0.25	2.83	1	0.005
Body size	0.53	0.2	2.59	1	0.010
Time*Connectivity	0.87	0.45	1.93	0.42	0.053
Juveniles' body growth					
Intercept	25.35	1.25	20.29	1	<0.001
Climate	2.66	1.42	1.88	0.85	0.061
Connectivity	3.08	1.52	2.02	1	0.043
Time	-3.51	0.65	5.37	1	<0.001
Birth date	-0.48	0.3	1.58	0.55	0.114
Body size	-2.31	0.38	6.00	1	<0.001
Sex	-2.61	0.51	5.08	1	<0.001
Climate*Connectivity	-2.66	2.03	1.31	0.4	0.191
Time*Climate	0.96	0.66	1.45	0.47	0.146
Time*Connectivity	1.53	0.65	2.33	1	0.020
Time*Climate*Connectivity	-1.6	1.15	1.39	0.08	0.165
Adults' body growth					
Intercept	4.61	0.36	12.65	1	<0.001
Climate	0.55	0.44	1.24	0.52	0.213
Connectivity	0.54	0.46	1.17	0.5	0.244
Body size	-3.76	0.14	27.22	1	<0.001
Sex	-4.02	0.28	14.46	1	<0.001
Climate*Connectivity	-0.39	0.82	0.47	0.13	0.635

Table S2.6 – Life-history traits: Effects of climatic conditions and connectivity treatments on probability of gravidity and body growth of juveniles and adults. All models included population identity as random intercept. Model analyzing juvenile body growth also included family identity as random intercept. Model analyzing adult body growth also included individual identity as random intercept

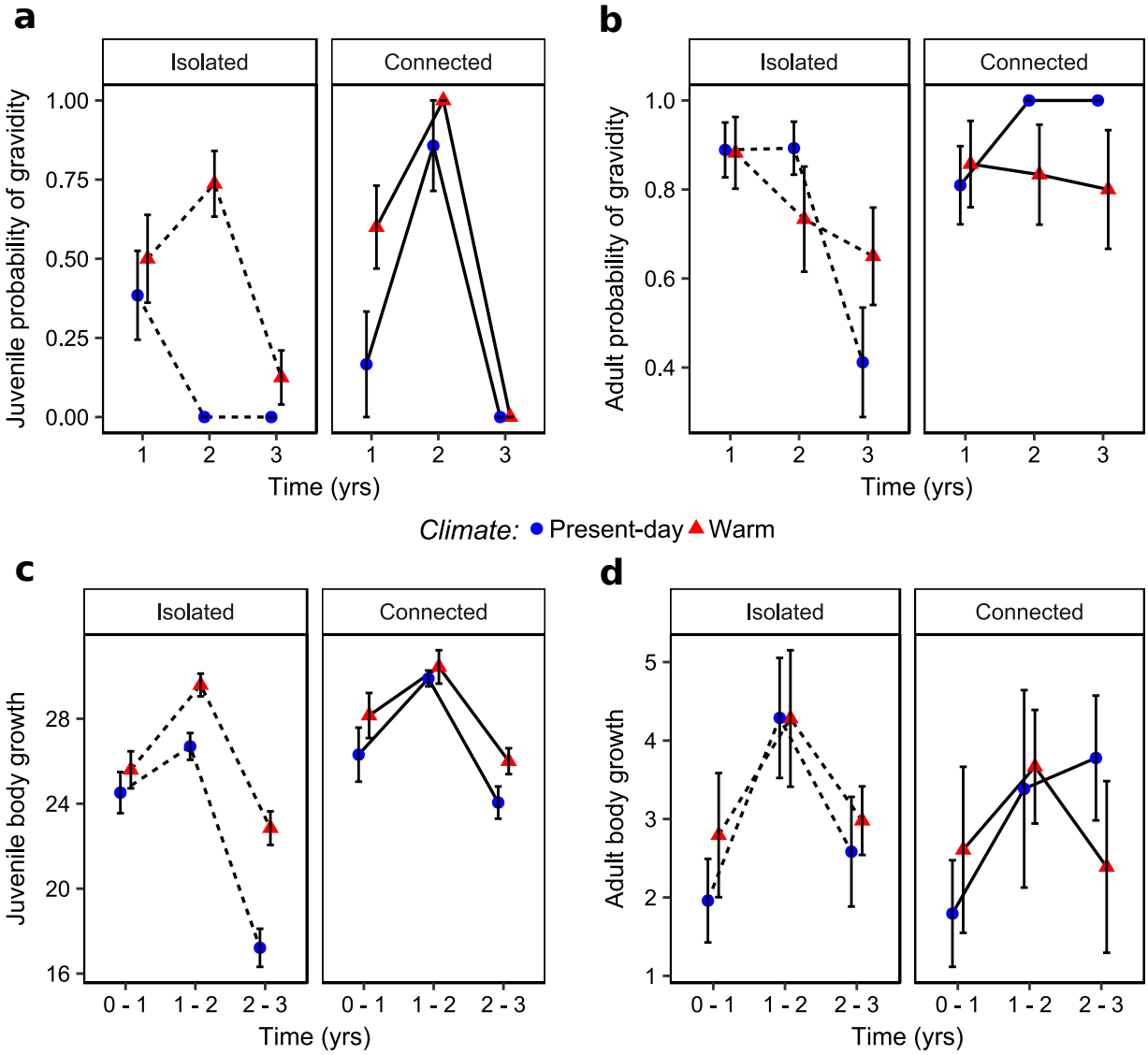

Figure S2.2 – Life-history traits: Juvenile probability of gravidity (a), adult probability of gravidity (b), juvenile body growth(c) and adult body growth (d) through time in isolated (dashed lines) and connected (solid lines) habitats under present-day (blue circles) and warm climate (red triangles). Mean ± SE are represented

Variable	Estimate	SE	z-value	RI	P-value
Adults' probability of gravidity					
Intercept	13.29	3.73	3.54	1	<0.001
Climate	6.61	3.28	1.99	0.52	0.046
Time	-5.35	1.24	4.29	1	<0.001
Body size	5.69	1.56	3.62	1	<0.001
Clutch size of adults					
Intercept	1.65	0.05	32.38	1	<0.001
Time	-0.15	0.05	-2.99	1	0.003
Body size	0.16	0.05	3.18	1	0.001
Survival probability of adults					
Intercept	0.06	0.44	0.14	1	0.889
Climate	-0.39	0.6	0.65	1	0.516
Time	-0.38	0.22	1.76	1	0.079
Body size	0.04	0.12	0.34	0.27	0.737
Sex	0.71	0.24	2.94	1	0.003
Time*Climate	0.72	0.27	2.68	1	0.007
Adults' body growth					
Intercept	4.89	0.39	12.47	1	<0.001
Climate	0.58	0.56	1.03	0.29	0.304
Time	-0.08	0.15	0.54	0.2	0.591
Body size	-4.17	0.17	24.84	1	<0.001
Sex	-4.22	0.37	11.36	1	<0.001

Table S2.7 – Life-history traits in isolated populations: Effects of climatic conditions on probability of gravidity, clutch size, survival probability and body growth of adults in isolated populations. All models included population identity as random intercept. Models analyzing adult probability of gravidity and body growth also included individual identity as random intercept

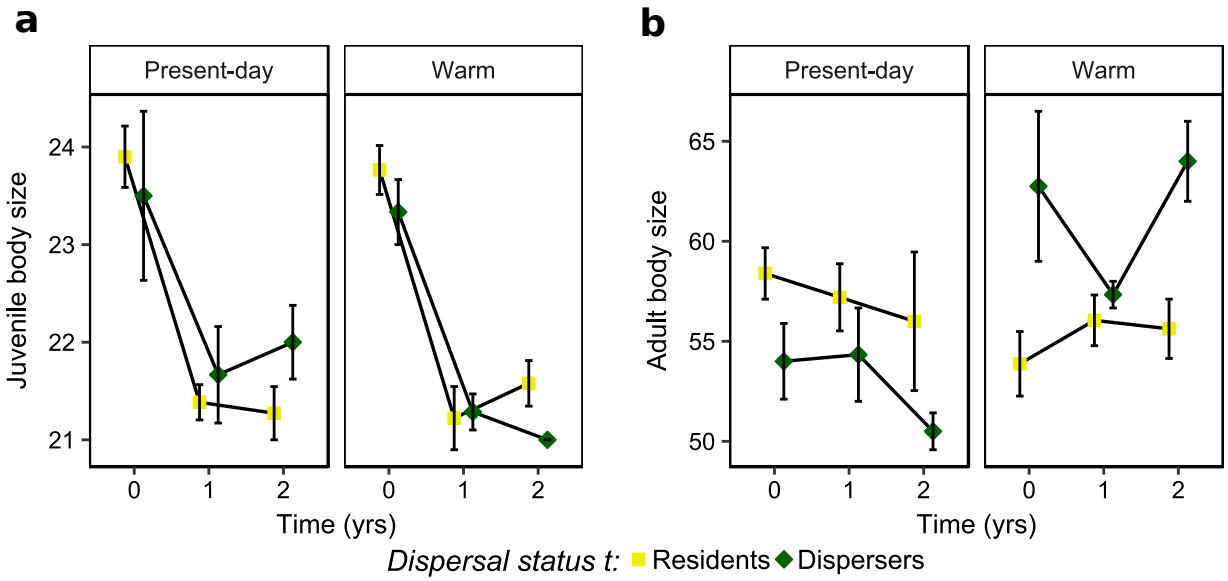

Figure S2.3 – Phenotype of dispersers: Juvenile body size (a) and adult body size (b)through time under present-day and warm climate for residents (yellow scares) and dispersers (green diamonds). Mean ± SE are represented

3 Influence of landscape connectivity on population response to climate change: dispersal and selection counteract phenotypic plasticity

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1 Abstract

Populations can respond to climate change by changing their geographic distribution and/or changing their phenotypic composition through phenotypic plasticity and evolutionary adaptation. Dispersal plays a central role in these responses as it allows to colonize new habitats and induces a gene flow affecting population composition. Dispersal could indeed hamper or promote genetic adaptation depending on the fitness consequences of dispersal movements. The fitness consequence of dispersal may further determine the relative influence of phenotypic plasticity and evolutionary adaptation. However, climate change is often associated with landscape fragmentation which impedes dispersal and may therefore shape the evolutionary processes underpinning population responses to climate change. Here, we experimentally investigated the impacts of a warmer climate on an ectotherm species distributed in landscapes varying in their habitat connectivity. We monitored populations of the common lizard (*Zootoca vivipara*) living in an experimental system where both climatic conditions (two climatic treatments: present-day and warm) and connectivity (two connectivity treatments: isolated and connected) were manipulated for three years. We quantified the influence of phenotypic plasticity and selection on phenotypic differences between climates, in the absence or presence of dispersal, focusing on three traits related to thermal physiology (dorsal darkness, thermal preference and daily emergence). We found that adult individuals became paler in warmer climate than in present-day climate, mostly in isolated populations. This phenotypic differentiation among climates mostly resulted from phenotypic plasticity in isolated populations, while the joint action of plasticity, selection and dispersal limit the phenotypic differentiation in connected populations. Whereas plasticity increased juvenile dorsal darkness in present-day climate relative to warmer climates, selection and dispersal acted in synergy to increase dorsal darkness in warm climate relative to present-day climate. Other thermal traits were weakly influenced by the climatic manipulation. Altogether, our results demonstrated that connectivity among habitats could modify the strength and direction of climate-dependent selection pressures on phenotypes. We thus call for future predictive

studies to better integrate dispersal and landscape structure when studying and predicting species response to climate change.

2 Introduction

Contemporary climate change is affecting biodiversity worldwide (Parmesan, 2006; Selwood *et al.*, 2015; Urban, 2015) and can lead to population and species extinction (Parmesan, 2006). Models predict the extinction of 5 to 37% of all species due to climate change depending on the geographic location (Thomas *et al.*, 2004; Urban, 2015). In addition to extinction, climate change also induces changes in the geographic distribution of populations which follow suitable climatic conditions in space. Chen *et al.* (2011) observed a shift of 11 meters per decade in altitude and 16.9 kilometres in latitude in response to climate change. Finally, climate change can induce a change in phenotypic composition of populations allowing them to persist under new climatic conditions (Parmesan, 2006; Lavergne *et al.*, 2010). The latter response to climate change relies on three main non-exclusive processes, namely phenotypic plasticity, evolutionary adaptation and dispersal.

Phenotypic plasticity is the ability of a genotype to produce different phenotypes in different environments (Pigliucci, 2001, 2005), and can be expressed in the form of reaction norms. Plasticity could thus modify population phenotypic distribution without any change in allele frequencies. Climate-driven phenotypic changes due to phenotypic plasticity have been observed in many studies (reviewed by Boutin & Lane, 2014; Charmantier & Gienapp, 2014; Crozier & Hutchings, 2014; Franks *et al.*, 2014; Reusch, 2014; Schilthuizen & Kellermann, 2014; Stoks *et al.*, 2014; Urban *et al.*, 2014). For example, great tit populations in the UK plastically advanced their laying date in response to warmer spring temperature (Charmantier *et al.*, 2008). Plasticity allows a fast response to environmental changes. However, the range of phenotypes which can be produced by plasticity is not infinite. Moreover, plasticity could be costly to develop (DeWitt *et al.*, 1998). Plasticity could therefore fail to continuously produce phenotypes able to cope with continuously changing environment (DeWitt *et al.*, 1998). Furthermore, climate change could modify the link between reaction norms and fitness, making initially adaptive plastic changes maladaptive (Visser, 2008; Charmantier & Gienapp, 2014). For instance, breeding time in a bird could be influenced by temperature as temperature de-

termine the period of higher abundance of caterpillar for their chicks. However, if the link between caterpillar abundance and temperature is modified, plastic response of bird to temperature could become maladaptive (Visser, 2008). Evolutionary adaptation is then needed to avoid population collapse.

Evolutionary adaptation affects population phenotypic distribution through changes in allele frequencies. Under climate change, some genotypes produce phenotypes better adapted than others to the new climatic conditions and should be favored by natural selection. Evolutionary adaptation could be fast enough to play a role in population responses to contemporary climate change. For example evolutionary adaptation accounted for 13% of the advance in the breeding timing of Canadian populations of red squirrels in response to increasing spring temperature (Réale *et al.*, 2003). However, evidence of evolutionary adaptation in response to climate change remains elusive because of the difficulty to disentangle it from phenotypic plasticity (e.g. Boutin & Lane, 2014; Charmantier & Gienapp, 2014; Gienapp *et al.*, 2008). Moreover, dispersal can further modulate the evolutionary adaptation to climate change by affecting population genetic composition.

Dispersal, the movement of individuals from birth site to breeding site or between two breeding sites (Howard, 1960), could indeed bring new phenotypes and genotypes into populations and change their composition. Individuals arriving into a population could bring either adaptive or maladaptive genes, promoting and swamping local adaptation respectively (Lenormand, 2002). Theory predicts that the swamping effect of dispersal from core population to margin populations could limit species distribution (Bridle & Vines, 2007). In the context of climate change, dispersal could either accelerate the phenotypic shift toward phenotypes better adapted to warmer conditions by bringing pre-adapted genotypes (at the cold margin mostly) or limit adaptation through a continuous flow of maladapted individuals (at the warm margin mostly). However, dispersal is a non-random process (Clobert *et al.*, 2001, 2012) made by particular individuals. Dispersers are often characterized by a combination of traits promoting movement (i.e. dispersal syndrome (Clobert *et al.*, 2009, 2012; Cote *et al.*, 2017)). Also dispersal is driven by the match between individuals' phenotype and their local environment: individuals with

sub-optimal phenotypes disperse to settle into more favorable conditions (i.e. matching habitat choice (Bowler & Benton, 2005; Edelaar *et al.*, 2008)). Gene flow associated with dispersal might thus be adaptive and promote phenotypic shift under climate change (Edelaar & Bolnick, 2012; Pellerin *et al.*, 2018). However, contemporary global changes often associate climate change and landscape fragmentation. Landscape fragmentation limits dispersal and could modify its role in population response to climate change.

Landscape fragmentation splits suitable habitats into a number of small and isolated patches (Wilcove *et al.*, 1986; Fahrig, 2003). As a result, dispersal among habitats and its associated gene flow decline through a decrease in the probability for individuals to find a suitable habitat and increasing their mortality during transience (Fahrig, 2003; Bonte *et al.*, 2012). Landscape fragmentation may thus reduce gene flow and its influence on phenotypic shift. Moreover, landscape fragmentation constrains individuals into their local habitat, preventing spatial range shift and enhancing selective pressures. The relative influence of phenotypic plasticity, evolutionary adaptation and dispersal on population phenotypic change should be shaped by landscape structure and the constraints to dispersal. As a consequence, studying the influence of phenotypic plasticity, evolutionary adaptation and dispersal together is crucial to better predict global change impacts on populations and biodiversity.

Here, we experimentally investigated the impacts of warmer climates on an ectotherm species distributed in habitats varying in their connectivity. Because their body temperature and hence their physiological functions strongly depend on external temperature, ectotherms are predicted to be especially sensitive to climate change (Dillon *et al.*, 2010). Climate change impacts should depend on each species thermal physiology, and recent studies claimed that tropical ectotherms should be particularly affected due to their low thermal safety margins (Huey *et al.*, 2010). However, within a species, individuals vary in their thermal phenotypes (e.g. thermal preference (Artacho *et al.*, 2013)). Phenotypic plasticity, evolutionary adaptation and dispersal could change thermal phenotypes distribution to help populations keep up with warmer temperatures (reviewed in Urban *et al.*, 2014). For instance, evolutionary adaptation changes the proportion of melanic morphs in

a beetle species in response to warmer spring temperature (Brakefield & De Jong, 2011) where melanism is involved in thermal regulation in this species. Thermal traits are also involved in dispersal decisions in ectotherms; in the common lizard (*Zootoca vivipara*), individuals with high thermal preference dispersed more from cooler habitats whereas individuals with low thermal preference dispersed more from warmer conditions (Bestion *et al.*, 2015a).

We monitored populations of common lizard (*Zootoca vivipara*) living in an experimental system where both climatic conditions and connectivity were manipulated for three years. We quantified the influence of phenotypic plasticity and evolutionary adaptation on phenotypic differences among climates, in absence or presence of dispersal, on three thermal traits, namely dorsal darkness, thermal preference (a good proxy of thermal optimum (Huey *et al.*, 2012)) and daily emergence. Despite the relative short period of time of the experiment (2 generations in our experiment), evolutionary adaptation could play a significant role in phenotypic differentiation given the low survival rate in the youngest age class (mean mortality over the first year of life: 90% (Avery, 1975), but the mean mortality was 0.74 in our experiment). Finally, we used a common garden experiment to test whether the changes in phenotypes over the three years of climatic and connectivity treatments resulted in differences in individuals' success in the different climatic conditions.

Although dorsal darkness is involved in complex processes (e.g. thermoregulation (Trullas *et al.*, 2007), UV protection (Roulin, 2014), resistance against pathogens (Côte *et al.*, 2018)), we expected it to decrease with warmer climate because darker individuals should be more at risk of overheating. Preference for warmer temperature should be promoted in warmer climatic conditions compared to cooler climatic conditions because individuals with higher thermal preference should better perform in warmer environment. Individuals should also emerge earlier in the morning in warm climate to avoid deleterious temperatures occurring later in the day (Sinervo *et al.*, 2010). Finally, common lizards may adjust their dispersal strategies to the climatic conditions according to their thermal phenotype (Lepetz *et al.*, 2009; Bestion *et al.*, 2015a). We thus expected con-

nectivity among habitats to promote spatial sorting of phenotypes, favoring population differentiation and local adaptation.

3 Materials and methods

3.1 Model species

The common lizard (*Zootoca vivipara*) is a small viviparous lacertid (adult snout-vent length = 50-70 mm) widespread across Eurasia where it inhabits peat bogs and heathland. Three age stages can be distinguished: juvenile (<1 year-old), yearlings (between 1 and 2 year-old) and adults (>2 year-old). The common lizard has been studied as a model ectotherm species for more than 20 years (Massot *et al.*, 1992; Cote & Clobert, 2007b; Le Galliard *et al.*, 2008), particularly to investigate the impact of contemporary climate change on population dynamics and population composition (Sorci & Clobert, 1999; Chamaillé-Jammes *et al.*, 2006; Marquis *et al.*, 2008; Le Galliard *et al.*, 2010; Bleu *et al.*, 2013; Bestion *et al.*, 2015b; Rutschmann *et al.*, 2016). The individuals used in this study were descendants of lizards captured in the Cevennes, France, in 2010 (2012-10 DREALE). Lizard populations were maintained in the Metatron (see next section) for several experiments (Bestion *et al.*, 2015a,b, 2017) and mixed regularly to prevent high levels of inbreeding. In our study system (Ariège, France), lizards hibernate from November to February and mate just after emergence. Females lay around 5 (1-12) soft-shelled eggs. Parturition starts in June and all parturition occurs within a one-month period on average. Juveniles emerge from the eggs within one hour after parturition and are immediately independent (Massot *et al.*, 1992).

3.2 Experimental design and population monitoring

We used the Metatron, an experimental system situated in the south of France (Ariège) composed of 48 interconnected semi-natural enclosures of 100 m^2 surface each (Legrand *et al.*, 2012). Tarpaulins buried in the soil and nets prevent terrestrial and avian predation and lizard escapes. Each enclosure acts as a mini-ecosystem with vegetation, insect

communities and habitat heterogeneity with rocks, wood logs and small water ponds. Enclosures can be connected through a 19 meters corridor, corresponding to the minimal dispersal distance of the common lizard (Clobert *et al.*, 1994). Temperature, hygrometry and illuminance are automatically recorded every 30 minutes. Temperature can be manipulated via motorized shutters and each enclosure can be watered through sprinklers. We developed two climatic treatments by closing the automatic shutters at different temperatures. For the "present-day climate" treatment, the shutters automatically closed when ambient temperature in the enclosures reached 28°C. For the "warm climate" treatment, the shutters closed when ambient temperature reached 38°C. Given that enclosures are intrinsically warmer than outside, the present-day climate treatment allows to obtain thermal conditions similar to the mean temperature outside of the Metatron (temperature in the nearby meteorological station of Saint-Girons Antichan (Bestion *et al.*, 2015b)). During the three years of our experiment, the mean summer daily temperatures in the warm climate treatment were on average 1.5°C warmer than the present-day climate treatment. As our treatments depend on outdoor climatic conditions, the treatments were efficient during the summer daytime (mid-June to mid September) and the difference between treatments varied with the weather. The mean summer temperature could therefore be slightly different between the years (mean ± sd, 26.23 ± 0.25 and 27.71 ± 0.26 in 2015, 26.34 ± 0.24 and 27.88 ± 0.24 in 2016, 25.52 ± 0.24 and 26.67 ± 0.25 in 2017 for present-day climate treatment and warm climate treatment respectively).

Our experimental design consisted in 16 enclosures with two climatic and two connectivity treatments. Eight pairs of enclosures combining a present-day enclosure and a warm climate enclosure were created. The corridor between the two enclosures was open for four pairs allowing lizards to move from one climatic treatment to the other (i.e. connected treatment) while the corridor was closed for the four remaining pairs preventing any movement (i.e. unconnected treatment). In the connected treatments, corridors were opened from March to mid-October spanning the entire period of lizards' activity. In 2017, we opened corridors by the end of March due to the maintenance of the system. However, it should not have much influence on connectivity as it covers a small period of

time.

The experiment started in 2015 and spanned 3 years. Early July 2015, 546 lizards (240 adults and yearlings and 306 juveniles) were released into the 16 enclosures. Populations in each enclosure were composed of 10 females, 5 males and 19 ± 1 juveniles, corresponding to intermediate density observed in natural populations and used in other semi-natural systems (Massot *et al.*, 1992; Cote & Clobert, 2007a). We split clutches among different enclosures to enhance genetic diversity within populations and released juveniles in enclosures without their mother to avoid kin competition. All the lizards present in the system were individually identified (i.e. marked by toe clipping) and measured for body size (i.e. snout-vent length) and thermal preference (see below), and a tail tip was taken for genetic identification and paternity analyses. Adults were also measured for dorsal darkness (see below) before being released. We ensured that there was no difference in age structure, body size, dorsal darkness and thermal preference between treatments (difference between treatments for all traits: $p > 0.55$). After 3 years of experiment, we did a reciprocal common garden experiment (see below) to test whether the changes in phenotypes resulted in differences in individuals' success in the different climatic conditions.

From 2016 to 2018, we applied the same protocol to monitor populations. In May, before females started laying eggs, all the individuals were recaptured from enclosures and brought back to the laboratory. They were identified, measured for body size and dorsal darkness and maintained in individual terraria (17x34x20 cm for adult females and gravid yearling females and 11x17x15 cm for males and non-gravid yearling females). Terraria contained a 3 cm sterilized litter layer, a petri dish with water, a piece of absorbent paper, a cardboard and a plastic tube as shelter. A light bulb (25 W) and an ultraviolet lamp (Zoomed Reptisun 5.0 UVB 36 W) provided heat for thermoregulation and light 6 h per day (from 9:00 to 12:00 and from 14:00 to 17:00). Lizards were lightly sprayed with water three times a day (in the morning, at mid-day, and in the evening) and offered two crickets (*Acheta domestica*) daily. After one week of acclimation to the laboratory conditions, all individuals were tested for their thermal preference and emergence (see below). Females laid eggs in their terrarium and the juveniles were isolated from their mother directly

after parturition. They were measured, weighted, marked and a tail tip was taken for genetic sampling. All juveniles were measured for thermal preference one day after birth, for emergence 2 days after birth and for dorsal darkness 3 days after birth.

3.3 Thermal preference test

Thermal preference test was performed in a controlled temperature room (18°C) in eight 100x20x40 cm glass arenas. Marks on the floor virtually divided each arena in ten 10 cm zones and a movable separation created a 10 cm acclimation zone at one end of the terrarium. At the opposite end of each arena, a light bulb (60W) created a thermal gradient from 40.0 ± 1.3°C to 19.2 ± 0.7°C. The temperature in each zone along the thermal gradient was recorded with thermometers. Individuals were maintained in the controlled temperature room without a heat and light source on the morning of the test, and were tested within few hours. This ensured that there were no differences in the motivation of animals to thermoregulate prior to the experiment and prevented differences due to hour of the day. Lizards were placed individually into the testing terrarium in the acclimation zone, at the coolest part of the temperature gradient, and left for 10 minutes to acclimatize before removing the separation. The separations were then removed and lizards could move in the arenas for 30 minutes. Video camera recorded the position of the lizard during the test. Each day, a maximum of 40 lizards could be measured in 5 sessions, from 8:30 to 12:30. Video data were analysed using The Observer 2.01 software. We calculated thermal preference as the mean of the temperature of the zones where the lizard stayed during the experiment weighted by the time spent at each position. In another study, we found that such thermal preference was repeatable over two weeks ($R = 0.43$ [0.19,0.54]) and was not related to other behavioural traits (p-value of the Pearson's correlation between traits: $p > 0.13$ for activity, exploration, sociability (Bestion *et al.*, 2015a)).

3.4 Dorsal darkness

Adult lizards were carefully positioned in a computer scanner (Canon CadoscanLide 110) lined with high density foam to avoid injuries. Pictures of dorsal patterns were taken at a resolution of 400 dpi. Pictures were analyzed using ImageJ software (Schneider *et al.*, 2012). Three zones were delimited on the back of the lizard, between front and rear legs: a central zone and two lateral zones (left and right) corresponding to the flanks. The picture was transformed in shades of grey and then in black and white according to a fixed grey threshold. The percentage of black pixels in each zone was computed. Darkness values corresponded to the average percentage of black of the three zones. A grey threshold value of 45 was chosen to maximize variance in darkness among individuals. Such measurement was reliable; a test on 46 adult individuals showed a good between-measurement correlation (Pearson's correlations, $r = 0.91$ [0.85, 0.95], $p < 0.001$). Moreover, this dorsal darkness was a good proxy of observed darkness, resulting from melanin-based coloration (San-Jose & Fitze, 2013), as a test on 164 adult individuals showed a good correlation between measured dorsal darkness and darkness scores attributed on a visual scale from 1 to 6 by an experimented observer ($r = 0.52$ [0.10, 0.63], $p < 0.001$).

In juveniles, the method was slightly different as their small size at birth did not allow us to scan them. Juveniles were softly maintained between two petri dishes and placed under binocular magnifier at x6.5 magnification. A circular lamp set at 10% of illuminance and fixed on the magnifier provided constant light conditions. A dorsal picture was taken with a camera fixed on the top of the magnifier. Pictures were then analyzed using imageJ software. One central zone was defined, positioned between the neck and the middle of the back. The flanks could not be measured because they were blurred. As for adults, the picture was transformed in shades of grey and then, in black and white. Because juveniles are darker than adult, the grey threshold was fixed at 30 to maximize the variance in darkness among individuals. Darkness values corresponded to the mean percentage of black pixels. Juvenile darkness was not measured in 2015 because the method was not yet available. However, given the number of juveniles and the split-clutch design, released juveniles were unlikely different among treatments.

3.5 Emergence

Emergence was defined as the time of the day at which individuals started to be active. Each 15 minutes from 8:45 AM (i.e. 15 minutes before the light was turned on) to 11:00 AM, an observer discretely passed in front of the terraria and recorded for each lizard if it was active (i.e. thermoregulating, immobile out of the shelter and ground or moving) or not. Emergence data were then converted in continuous time from 0 to 135 minutes. Emergence of reproductive females and of other individuals was measured in separate rooms due to technical constraints. Temperature of both rooms where maintained constant (18°C). Emergence was not measured in 2015 for juveniles. Emergence was repeatable over 2 days in adults (R=0.504 [0.446;0.541], $p < 0.001$) and juveniles (R=0.27 [0.207,0.333], $p < 0.001$).

3.6 Monitoring of life history and phenotypic traits

Early July, all males, females and their clutch were released into the Metatron after phenotypic measurements. We released adult individuals back to the enclosure where they were captured from in May and juvenile individuals in the same enclosure as their mother. Over the course of the experiment, three populations went extinct (two in 2016, one present-day and one warm enclosures; One present-day enclosure in 2017), reducing the total number of populations from 16 to 13. In mid-September, individuals were captured during three capture-release-recapture sessions. Three captures allow to capture at least 93% of survivors (Bestion *et al.*, 2015b). All captured individuals were identified to determine summer survival probability and dispersal for each individual, and then released back into their enclosures for hibernation. Annual survival was measured by capturing all survivors in May the year after the release. From these captures, we could further identify individuals which dispersed between connected enclosures. All individuals were then measured for phenotypic traits, as described above, allowing to estimate phenotypic plasticity for each trait.

3.7 Reciprocal common garden

In July 2018, individuals were distributed into 12 enclosures, 6 with a present-day climate treatment and 6 with a future warm climate treatment. All enclosures were isolated (no connectivity between enclosures). Each population was composed of 10 ± 1 females, 10± 1 males and 14 ± 1 juveniles. We mixed individuals from the different connectivity and climate treatments so that half of the individuals belonging to each pair of treatments were released into present-day climate, and the other half in warm climate. There was also no significant difference in age structure, body size, thermal preference, emergence and darkness between individuals released in present-day and warmer climates (difference between treatments for all traits: $p > 0.86$ except emergence for which $p > 0.14$). Further, lizards were not released in their enclosure of origin, or for connected enclosures between 2015 and 2018, in the enclosure paired with the enclosure of origin. All individuals were therefore naïve about the enclosure of release. For juveniles, siblings of each clutch were split into different enclosures of present-day and warm climate treatments avoiding the enclosure in which their mother was released. In September 2018, all individuals were captured and brought back to the laboratory through 10 capture sessions. This protocol, used every year in May, allows capturing all survivors. The survival status of each individual was determined and individuals were measured for body size and weight.

As we did not measure thermal phenotypes at the end of the common garden, it did not allow us to distinguish between plastic and evolutionary processes behind the phenotypic changes induced by our 3 years of treatments. However, it allowed to test whether the changes in phenotypes resulted in differences in individuals' success in the different climatic conditions. The present common garden can thus be seen as an adaptation test.

3.8 Statistical analyses

We analyzed juveniles separately from adults and yearlings, hereafter encompassed in the term "adults".

Thermal phenotypes

In a first step, we studied the influence of climatic and connectivity treatments on adult and juvenile phenotypes in 2018, after three years of manipulation. We analyzed the influence of experimental treatments on dorsal darkness and thermal preference using linear mixed models and on emergence using survival models with random effects for truncated data. Some individuals were indeed never seen during the emergence test and had therefore a truncated data as emergence. Independent variables included climatic treatment, connectivity treatment and their interaction. We also included sex, body size and age class (yearling and adult) for adults, and sex, body size and birth date in Julian day for juveniles into the models. Random intercept included enclosure identity to account for the dependency of individuals of the same population and family identity for analyses on juveniles as sibs from the same clutch were not independent. We included the session and arena identities as random intercept when analyzing thermal preference and the room identity as a fixed factor when analyzing emergence.

We also analyzed thermal phenotypes in isolated and connected population separately using the same model structures.

Adaptive processes

In a second step, we studied the evolutionary processes (i.e. plasticity, selection and dispersal) explaining the potential phenotypic differences after three years of manipulation. To do so, we studied lifetime individual phenotypic changes and climate-dependent relationships between phenotype, survival and dispersal.

First, we studied the influence of climatic and connectivity treatments on the plasticity in dorsal darkness, thermal preference and emergence of adults and juveniles using linear mixed models. Trait plasticity was measured as the difference, for a surviving individual, between its trait value at May year t+1 and its trait value at May year t. For juvenile dorsal darkness, plasticity was calculated on centered and scaled values because methods to estimate dorsal darkness at birth and at one year-old were different. For emergence, truncated data were arbitrarily fixed at 140 minutes. Emergence data

were log transformed because of normality issues in plasticity for emergence. All models included climatic treatment, connectivity treatment and their interaction. Independent variables also included time, sex and body growth over one year for juveniles and adults, birth date for juveniles only and age class (i.e. yearling and adult) for adults only. Time was treated as a categorical variable to account for non linear response of plasticity due to variability among the years. We further added, as a random intercept, enclosure identity and individual identity in the analyses where individuals could appear more than once (i.e. individuals surviving more than one year) and family identity in analyses on juveniles, as sibs from the same clutch were not independent. Considering that dispersers experienced both climatic conditions, we excluded dispersers from these analyses. We also analyzed plasticity in thermal traits in isolated and connected populations separately using the same model structures.

Second, we calculated selection gradients and selection differentials in the different experimental conditions, using survival as the fitness variable. Gradients and differentials allow to distinguish between selection acting directly on the character (selection gradient) and correlative selection (selection differential (Lande & Arnold, 1983)). We used a multiple step process to calculate selection gradients. (i) We used a generalized mixed model with binomial distribution and logit link, with survival as dependent variable and all three-way interactions of thermal traits, climatic conditions and connectivity treatment as independent variables. We added time, sex, and body size in every model, age class for adults and birth date for juveniles. Enclosure identity, individual identity in the analyses where individuals could appear more than once and family identity in the analyses on juveniles were added as random intercept. (ii) We further explored if stabilizing or disruptive selection could shape population phenotype composition. To do so, we added one three way interaction including quadratic term of one thermal trait, climatic condition and connectivity treatment to the model developed in the previous step. We compared models with a quadratic term to models without it and kept the model with the lowest AIC. In all analyses, the best model was the one without quadratic term. Then the collinearity of the different variables of the models was quantified using variance infla-

tor factors (VIF). VIF was <10 in all models, indicating low collinearity (Montgomery *et al.* (2012), but see Zuur *et al.* (2010)). Moreover, we obtained similar results when running separate models with the different thermal traits one by one, supporting the fact that covariations among traits did not influence the results. (iii) We selected the best model structure (see below for selection procedure). When interactions regarding thermal traits, climatic conditions and connectivity treatments were selected in the best model, we explored the influence of thermal traits on survival in each combination of treatments present in these interactions by running the best selected model in each combination of treatments. (iv) Then, we calculated selection gradients in each of our four combinations of treatment with generalized mixed models with survival as dependent variable, and the three thermal traits as independent variables (Lande & Arnold, 1983), plus the covariates kept in the best model in step (iii). Random structure of these models was also the one selected in step (iii). Estimates of these logistic models were transformed into average gradient vectors $\beta avggrad$ given that the dependent variable was binary (Janzen & Stern, 1998). Selection differentials were calculated as the difference between the mean phenotype of survivors and the mean phenotype of the population, before the selective event (Lush, 1937; Morrissey *et al.*, 2010). Phenotypic values were standardized (mean = 0; $\sigma^2 = 1$) to allow between-trait comparisons of selection differentials. Selection gradients and differential were calculated on summer and annual survival of adults and juveniles excluding dispersers.

To quantify selection response, we also calculated heritability of each thermal trait. We used MCMCglmm in an animal model to decompose additive variance (V_A), maternal variance (V_M) environmental variance (V_E) and residual variance (V_R) for dorsal darkness, preferred temperature and emergence at birth. The model was run on natal phenotype of juveniles from 2015 (for thermal preference), 2016, 2017 and 2018. We included year as a fixed effect and animal, mother identity and parents' population identity as random effects. The parents' population identity allows estimating the environmental variance. Using the variances, we calculated heritability (mean h^2 and 95% confident interval) and coefficients of additive genetic variation (CV_A) as a measure of evolvability (Hansen *et al.*,

2003).We also compared the DIC of the best model with the DIC of the model without animal effect.

Third, we explored climate x phenotype-dependent dispersal in connected enclosures using generalized mixed models with binomial distribution and logit link to analyze the effects of phenotypic traits and climatic condition on summer and annual dispersal probability. Independent variables included the three two-way interactions between thermal traits and the climatic conditions. Independent variables also included time, sex, body size, birth date (juvenile only) and age class (adults only). Random intercepts included enclosure identity and family identity for analyses on juveniles.

Common garden

Finally, we analyzed survival during the common garden experiment using generalized mixed models with binomial distribution and logit link. Models included the climatic conditions during the 3 years of the main experiment, connectivity during the main experiment, climatic conditions during the common garden experiment and their interaction. Independent variables also included sex, body size, age class (for adults only) and birth date (for juveniles only). Random intercepts included the identity of enclosures both during the 3-year experiment and during the common garden, and family identity in analysis on juveniles. In a second step, we also developed models integrating individual phenotypes. However, due to the low number of juveniles, models have been performed on adults only. Individuals from isolated and connected populations were analyzed separately to avoid four-way interactions. Models included survival as dependent variable and all three way interactions linking thermal traits, climatic conditions during the 3 years of the main experiment, and climatic conditions during the common garden experiment. Independent variables included sex, body size and age class. Random intercepts included the identity of enclosures both during the 3 years experiment and during the common garden.

Model selection procedure

Model selection was performed using the following procedure. Full models with all fixed variables and random effects were built and random structure of each model was selected by AIC, following Zuur *et al.* (2009). Random structure (including structure without random effect) minimizing AIC was then selected. All possible models of different fixed effects were built and ranked by AIC and conditional estimates, standard errors, z-value, relative importance and p-value of all variables present in best models within a delta AIC of 2 were obtained through model averaging procedure (Burnham *et al.*, 2011).

All analyses were performed using R software version 3.4.3 (http://cran.r-project.org/) with lme4, survival, coxme (survival models for emergence), MCMCglmmm (for heritability) and MuMin packages.

4 Results

4.1 Thermal phenotype

Three years of climatic treatment had contrasted influence on the thermal phenotype of adult and juvenile individuals. At the end of the experiment, adult individuals were darker in present-day climate than lizards in warm climate (Table 3.1, Figure 3.1a). The difference in adult dorsal darkness among climates was mostly observed in isolated population (Tables S3.1, S3.2) but the interaction between climate and connectivity was not retained in the best model (Table 3.1). In juveniles, individuals were also darker in present day climate than in warm climate (Table 3.1, Figure 3.1b), mostly in isolated populations (Tables S3.1, S3.2). Climatic conditions had a very weak effect on thermal preference of adults and juveniles and on emergence of adults (RI < 0.3, Table 3.1, Figure 3.1c,e); adults preferred slightly lower temperature in warm climate than in present day-climate, mostly in isolated populations (Tables S3.1, S3.2). They also emerged slightly later in warm climate, in connected population only (Tables S3.1, S3.2). Conversely, juveniles preferred slightly higher temperature in warm climate than in present day climate, mostly in iso-

lated populations (Figure 3.1d, Tables S3.1, S3.2), and showed no difference in emergence among climates (Table 3.1, Figure 3.1f).

4.2 Phenotypic plasticity

Overall, the link between plasticity in thermal traits and the climatic conditions was weak (Tables 3.2, 3.3, Figure 3.2). However, both juvenile and adult individuals became darker in present day climate than in warm climate (RI = 0.35 and RI = 0.4 for adults and juveniles respectively, Tables 3.2, 3.3, Figure 3.2a,b). In adults, individuals became darker in present-day than in warm climate mostly in isolated populations (Tables S3.3, S3.4). Juvenile individuals also developed higher thermal preference in warm climate than in present day climate, mostly in connected populations (Figure 3.2d, Tables 3.3, S3.3, S3.4). Finally, juvenile individuals decreased their emergence over one year in present-day climate but not in warm climate, in isolated populations only (Figure 3.2f, Tables 3.3, S3.3, S3.4).

4.3 Selection

Summer survival of adults was not influenced by climatic conditions or their interaction with thermal traits (Table 3.4). However, dorsal darkness and, to a lower strength, thermal preference interacted with connectivity to influence survival (Table 3.4, Figure S3.1). When conducting analysis separately in isolated and connected populations, there was no significant influence of dorsal darkness on survival in both conditions (isolated populations: estimate = -0.17, p = 0.412; connected populations: estimate = 0.22, p = 0.234). In connected populations, there was a marginally significant negative effect of thermal preference on survival (estimate = -0.352, p = 0.062) whereas the relation was not significant in isolated populations (estimate = 0.10, p = 0.629). In juveniles, the three-way interaction between climatic conditions, connectivity and dorsal darkness affected summer survival (Table 3.4, Figure 3.3). When running the global average model in each condition, dorsal darkness had a significant positive effect on survival (estimate = 1.06, p = 0.026) in warm climatic conditions and a significant negative influence on survival

(estimate = -0.66, p = 0.042) in present-day climate when populations were connected. In isolated populations, there was no significant influence of dorsal darkness on survival, but we observed that selection appeared to be reversed in comparison to selection in connected populations (present-day: estimate = 0.22, p = 0.516; warm: estimate = -0.26, p = 0.522).

Annual survival of adults was affected by the interaction between thermal preference and connectivity (Table S3.5, Figure S3.2a), and by the interaction between climatic conditions and emergence (weaker effect, RI = 0.45, Table S3.5, Figure S3.2b). The three-way interaction between climatic conditions, connectivity and thermal preference was also in the averaged best model but had a very weak relative importance (RI=0.09, Table S3.5). In isolated populations, thermal preference had a marginally significant positive effect on survival (estimate = 0.26, p = 0.077) whereas there was no effect in connected populations (estimate = -0.24, p = 0.147). In present-day climate, emergence had a marginally significant positive effect on survival (estimate = 0.32, p = 0.065). There was no effect of emergence on survival under warm climate (estimate=0.09, P=0.851). Annual survival of juveniles was very weakly influenced by the interacting effect of connectivity and dorsal darkness (RI = 0.08, Table S3.5). There was no other differential influence of thermal traits on survival among climatic conditions or connectivity treatments.

In adults, the only significant selection gradient calculated on summer survival was a negative selection gradient on thermal preference under present-day climatic conditions in connected populations ($\beta avggrad$ = -0.12 [-0.22;-0.02], Table S3.6). In juveniles, there was a significant negative selection gradient on dorsal darkness under present-day climate ($\beta avggrad$ = -0.14 [-0.28;-0.01], Table S3.7) and a significant positive selection gradient under warm climate ($\beta avggrad$ = 0.17 [0.02;0.31], Table S3.7) in connected populations. Over one year, there was a weak positive selection gradient on thermal preference of adults under present-day climatic conditions in isolated populations ($\beta avggrad$ = 0.06 [0;0.13], Table S3.8). The gradient was significantly negative under present-day climatic conditions in connected populations ($\beta avggrad$ = -0.11 [-0.2;-0.01], Table S3.8). In juveniles, the only significant selection gradient over one year concerned dorsal darkness in connected

populations, under warm climate ($\beta avggrad$ = 0.12 [0.01;0.24], Table S3.9). Overall, selection differentials were consistent with selection gradients (Tables S3.6, S3.7, S3.8, S3.9). However, in juveniles, selection differentials of thermal preference calculated on annual survival were relatively high (between 0.14 an 0.25) whereas selection differential where small and non significant (Table S3.9).

Finally, all traits were heritable with h^2 of 0.25 ([0.10;0.41]), 0.18 ([0.05;0.35]) and 0.22 ([0.05;0.46]) for dorsal darkness, thermal preference and emergence respectively (Table S3.10).

4.4 Dispersal

Adult summer dispersal (i.e. the period during which the climatic treatment occurred) was driven by the interaction between thermal preference and climatic conditions in adults (Table 3.5, Figure 3.4c). Dispersers from present-day climate had higher thermal preference than residents of the present-day climate. Conversely, dispersers from warm climate had lower thermal preference than residents in warm climate (Figure 3.4c). Dispersal from warm to present-day climate was also influenced by emergence in adults. Dispersers emerged earlier than resident individuals of the warm climate. There was no difference in emergence between dispersers and residents of the present-day climate (Figure 3.4e, Table 3.5). However, the climate dependent effect of emergence on dispersal was weak (RI = 0.34, Table 3.5). In juveniles, dispersal was driven by the interaction between dorsal darkness and climatic conditions. Dispersers were darker than residents in present-day climate treatment and lighter than residents in the warm climate treatment (Table 3.5, Figure 3.4b). Juveniles dispersing from warm climate treatment also preferred higher temperature than residents. However the effect of thermal preference, depending on the climatic conditions, on juvenile dispersal was weak (RI = 0.11, Table 3.5).

Dispersal pattern over one year was consistent with summer dispersal pattern. Indeed, one-year dispersal was also influenced by the interacting effect of climatic conditions and thermal preference in adults (Table S3.11, Figure S3.3). In Juveniles, the interacting effect of climatic conditions and dorsal darkness on summer dispersal was also maintained over

one year (Table S3.11, Figure S3.3).

4.5 Common garden

Adult and juvenile survival during the common garden was not dependent on the interaction between their climatic treatments or connectivity treatment during the experiment and the climatic conditions during the common garden (Table S3.12). However, climatic treatments during the three-year experiment interacted with adult phenotype to influence survival during the common garden. Summer survival of individuals from connected populations depended on the interaction between their previous treatment and their dorsal darkness (Table 3.6). Darker adults after three years in the present day climatic treatment better survived independently of the climatic condition during the common garden. Conversely, darker adults after three years in the warm climatic treatment had a lower survival independently of the climatic condition during the common garden (Table 3.6). For individuals coming from isolated populations, emergence positively affected summer survival in present-day enclosures of the common garden, but not in warm enclosures. Emergence also interacted with previous climatic treatment to affect summer survival. The three way interaction between emergence, climatic treatment during the experiment and climatic treatment during the common garden was kept in the best model, but had a very weak relative importance (RI = 0.02). Two way interactions between dorsal darkness and climate during the common garden, dorsal darkness and the three-year climatic treatment, and thermal preference and the three-year climatic treatment were also present in the best model but had a weak effect (RI<0.25, Table 3.6).

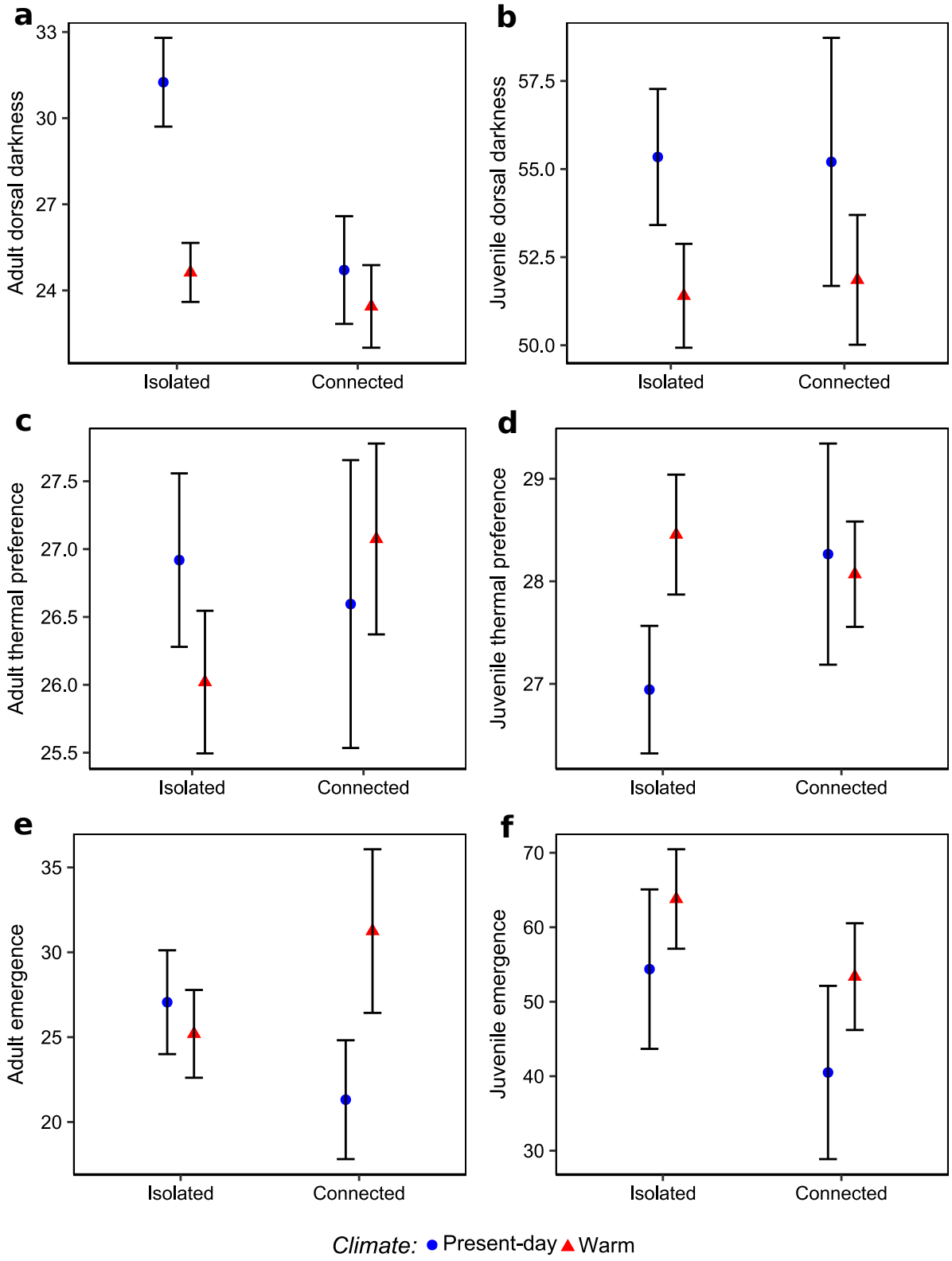

Figure 3.1 – Thermal traits of adults (a,c,e) and juveniles (b,d,e) after three years of climatic and connectivity treatments. Dorsal darkness (a,b), thermal preference (c,d) and daily emergence (e,f) in isolated and connected populations of present-day (blue circles) and warm (red triangles) climatic conditions. Mean ± SE are represented

Variable	Estimate	SE	z-value	P-value	RI
Adult dorsal darkness					
Intercept	29.95	2.64	11.30	<0.001	1
Age	-9.49	3.14	3.01	0.003	1
Body size	-2.40	1.34	1.78	0.075	0.72
Sex	4.17	1.45	2.87	0.004	1
Climate	-4.64	2.49	1.85	0.065	0.71
Adult thermal preference					
Intercept	25.06	1.13	22.06	<0.001	1
Body size	1.35	0.57	2.37	0.018	1
Sex	2.45	0.63	3.85	<0.001	1
Age	1.65	1.14	1.45	0.148	0.42
Connectivity	0.51	0.61	0.83	0.406	0.15
Climate	-0.52	0.63	0.82	0.415	0.27
Adult emergence					
Sexe	0.17	0.15	1.16	0.247	0.28
Body size	-0.07	0.08	0.89	0.372	0.18
Connectivity	0.01	0.28	0.03	0.973	0.25
Emergence room	0.13	0.16	0.80	0.423	0.09
Climate	0.03	0.22	0.14	0.892	0.16
Climate*Connectivity	-0.56	0.35	1.60	0.111	0.08
Age	0.04	0.15	0.24	0.812	0.07
Juvenile dorsal darkness					
Intercept	51.72	2.83	18.13	<0.001	1
Birth date	4.25	1.63	2.59	0.010	1
Sex	4.23	1.65	2.53	0.011	1
Climate	-5.06	3.06	1.64	0.101	0.6
Connectivity	6.18	3.22	1.90	0.057	0.69
Body size	-1.12	1.16	0.96	0.338	0.16
Juvenile thermal preference					
Intercept	27.97	0.84	32.82	<0.001	1
Body size	0.81	0.35	2.30	0.022	1
Sex	-0.50	0.58	0.85	0.398	0.24
Climate	0.70	0.87	0.79	0.429	0.23
Juvenile emergence					
Body size	0.39	0.10	3.74	<0.001	1
Sex	0.29	0.19	1.51	0.130	0.58
Birth date	0.05	0.09	0.53	0.595	0.25
Connectivity	0.06	0.19	0.30	0.765	0.12

Table 3.1 – Thermal traits of adults and juveniles after three years of climatic and connectivity treatments. The random structure of models are as follow. Adult dorsal darkness: enclosure identity; Adult thermal preference: enclosure identity, session and arena identity; Adult emergence: enclosure identity; Juveniles dorsal darkness: family identity; Juvenile thermal preference: family identity, session and arena identity; Juvenile emergence: enclosure identity

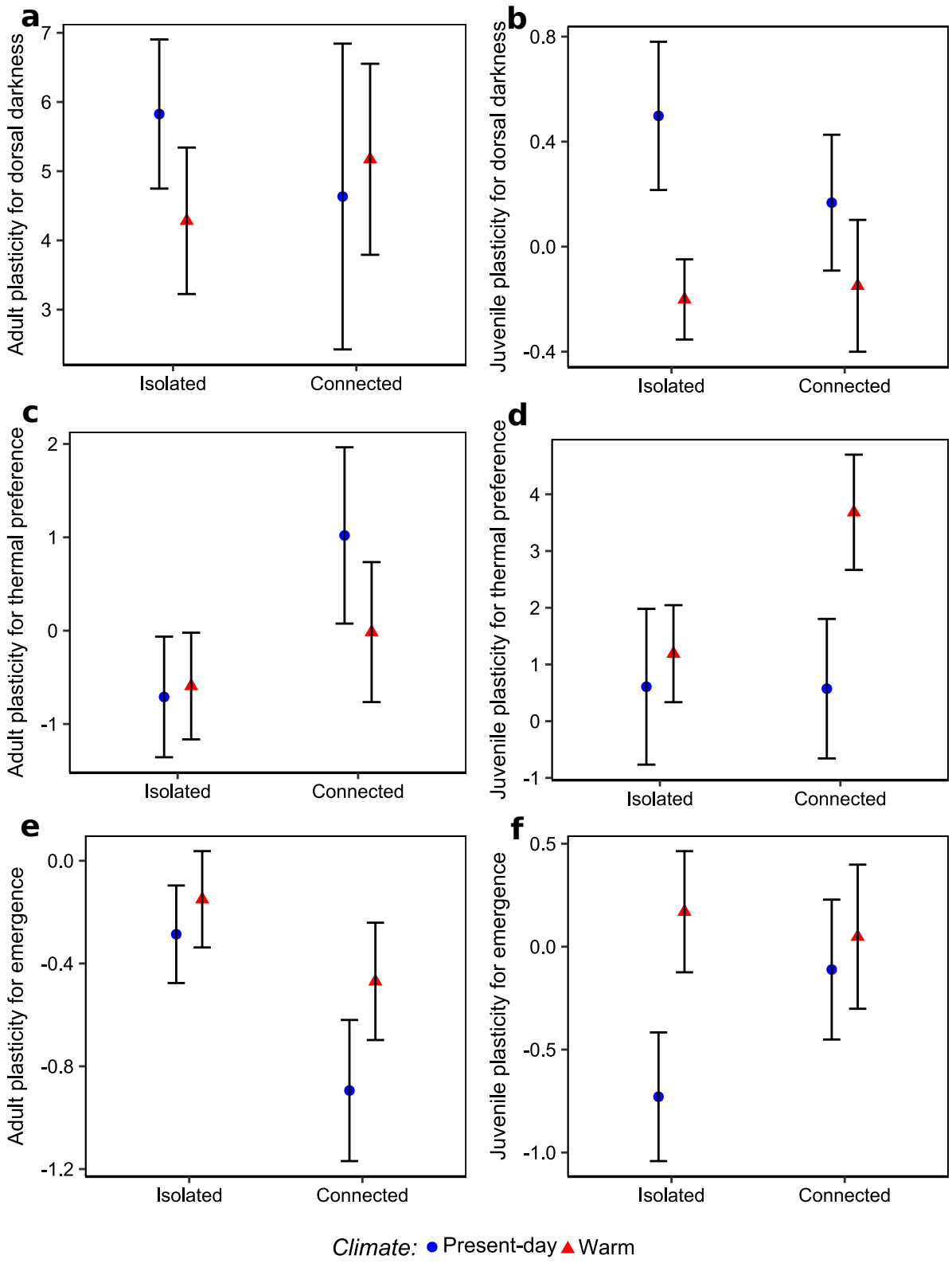

Figure 3.2 – Plasticity in thermal traits of adults (a,c,e) and juveniles (b,d,e) averaged over the three years of experiment. Plasticity in dorsal darkness (a,b), thermal preference (c,d) and daily emergence (e,f) in isolated and connected populations of present-day (blue circles) and warm (red triangles) climatic conditions. Mean ± SE are represented

Variable	Estimate	SE	z-value	P-value	RI
Adult plasticity for dorsal darkness					
Intercept	3.17	1.43	2.20	0.028	1
Age	3.13	1.25	2.50	0.013	1
Year2	-4.45	1.55	2.85	0.004	1
Year3	2.12	1.50	1.41	0.159	1
Sex	2.59	1.24	2.08	0.038	1
Climate	-1.52	1.26	1.21	0.227	0.35
Connectivity	0.47	1.35	0.35	0.728	0.18
Adult plasticity for thermal preference					
Intercept	-0.01	0.68	0.01	0.993	1
Year2	0.91	0.86	1.05	0.294	1
Year3	-1.84	0.83	2.19	0.028	1
Connectivity	0.79	0.75	1.06	0.290	0.25
Sex	0.54	0.69	0.78	0.436	0.19
Age	-0.24	0.69	0.35	0.729	0.15
Adult plasticity for emergence					
Intercept	-0.60	0.20	3.04	0.002	1
Year2	-0.48	0.25	1.91	0.056	1
Year3	1.08	0.24	4.45	0.000	1
Connectivity	-0.25	0.22	1.16	0.246	0.24
Sex	0.11	0.20	0.53	0.598	0.14
Body growth	0.05	0.11	0.45	0.652	0.14
Climate	0.08	0.20	0.39	0.693	0.13

Table 3.2 – Plasticity in thermal traits of adults after three years of climatic and connectivity treatments. The random structure for all model was without random intercept

Variable	Estimate	SE	z-value	P-value	RI
Juvenile plasticity for dorsal darkness					
Intercept	0.55	0.29	1.86	0.063	1
Year3	-1.07	0.35	3.02	0.003	1
Body growth	-0.48	0.15	3.22	0.001	1
Birth date	-0.63	0.14	4.56	0.000	1
Sex	0.33	0.18	1.8	0.072	0.68
Climate	-0.37	0.27	1.34	0.181	0.4
Connectivity	0.15	0.28	0.52	0.601	0.11
juvenile plasticity for thermal preference					
Intercept	3.08	1.25	2.45	0.014	1
Year3	-4.68	1.14	4.07	0.000	1
Climate	1.3	1.33	0.97	0.330	0.61
Connectivity	1.09	1.53	0.71	0.479	0.62
Climate*Connectivity	2.82	2.14	1.31	0.191	0.22
Sex	1.16	1.02	1.12	0.263	0.35
Birth date	-0.48	0.57	0.84	0.400	0.12
Body growth	0.86	0.64	1.33	0.184	0.12
Juvenile plasticity for emergence					
Intercept	-0.85	0.39	2.16	0.031	1
Year3	1.02	0.42	2.41	0.016	0.58
Birth date	0.41	0.21	2	0.045	0.8
Climate	0.8	0.51	1.58	0.114	0.7
Sex	0.37	0.33	1.12	0.261	0.17
Body growth	-0.46	0.24	1.87	0.061	0.56
Connectivity	0.82	0.59	1.37	0.170	0.27
Climate*Connectivity	-1.06	0.72	1.46	0.145	0.14

Table 3.3 – Plasticity in thermal traits of juveniles after three years of climatic and connectivity treatments. The best random structure for all model was without random intercept, except for plasticity in dorsal darkness where family identity was modeled as random intercept

Variable	Estimate	SE	z-value	P-value	RI
Adult summer survival probability					
Intercept	2.13	0.53	3.99	<0.001	1
Age	-0.55	0.35	1.54	0.125	0.57
Year2	-0.79	0.33	2.40	0.017	0.84
Year3	-0.46	0.36	1.28	0.201	0.84
Dorsal darkness	-0.30	0.19	1.59	0.111	0.92
Body size	-0.44	0.21	2.12	0.034	1
Thermal preference	-0.20	0.19	1.04	0.297	1
Connectivity	-0.50	0.57	0.87	0.387	0.92
Connectivity*Dorsal darkness	0.62	0.24	2.54	0.011	0.92
Connectivity*Thermal preference	-0.38	0.24	1.54	0.123	0.52
Sex	-0.23	0.31	0.73	0.463	0.14
Emergence	0.05	0.13	0.40	0.692	0.06
Juvenile summer survival probability					
Intercept	1.14	0.71	1.60	0.109	1
Dorsal darkness	0.84	0.25	3.40	0.001	1
Climate	-0.38	0.98	0.39	0.699	1
Connectivity	-1.10	0.93	1.19	0.236	1
Climate*Dorsal darkness	-0.91	0.31	2.89	0.004	1
Connectivity*Dorsal darkness	-1.35	0.34	3.95	<0.001	1
Climate*Connectivity	0.57	1.30	0.44	0.658	1
Climate*Connectivity*Dorsal darkness	1.30	0.45	2.86	0.004	1
Emergence	-0.12	0.10	1.21	0.226	0.19
Body size	0.09	0.11	0.82	0.414	0.13
Thermal preference	-0.13	0.15	0.88	0.377	0.21
Year3	-0.20	0.34	0.58	0.562	0.11
Birth date	0.07	0.13	0.57	0.571	0.11
Climate*Thermal preference	0.29	0.21	1.36	0.175	0.1

Table 3.4 – Summer survival of adults and juveniles. The random structure of models are as follow. Adult summer survival probability: enclosure identity; Juvenile summer survival probability: enclosure identity and family identity

Variable	Estimate	SE	z-value	P-value	RI
Adult summer dispersal					
Intercept	-1.95	0.48	4.01	<0.001	1
Dorsal darkness	-0.40	0.25	1.58	0.114	0.64
Thermal preference	0.88	0.35	2.53	0.012	1
Climate	-0.56	0.50	1.13	0.259	1
Climate*Thermal preference	-1.35	0.51	2.62	0.009	1
Emergence	0.20	0.32	0.63	0.528	0.39
Climate*Emergence	-1.13	0.64	1.75	0.080	0.34
Year2	0.93	0.54	1.70	0.088	0.35
Year3	0.20	0.68	0.30	0.767	0.35
Body size	-0.15	0.24	0.62	0.533	0.1
Sex	0.32	0.50	0.65	0.516	0.1
Juvenile summer dispersal					
Intercept	-2.16	0.58	3.69	<0.001	1
Dorsal darkness	0.72	0.4	1.81	0.070	1
Sex	1.26	0.59	2.12	0.034	1
Climate	-1.85	0.87	2.12	0.034	1
Climate*Dorsal darkness	-1.52	0.84	1.81	0.071	1
Year3	-1.1	0.89	1.23	0.218	0.39
Thermal preference	0.33	0.32	1.04	0.300	0.49
Climate*Thermal preference	1.02	0.98	1.04	0.300	0.11

Table 3.5 – Summer dispersal probability of adults and juveniles. The random structure of models are as follow. Adult summer dispersal: NA; Juvenile summer dispersal: NA

Variable	Estimate	SE	z-value	P-value	RI
Common garden - Adult summer survival - isolated populations					
Intercept	3.47	1.45	2.38	0.017	1
Emergence	2.41	1.3	1.83	0.067	1
Thermal preference	0.51	0.37	1.36	0.175	0.69
Climate exp	-1.1	0.79	1.37	0.169	0.85
Climate common garden	-0.74	1.53	0.48	0.631	0.87
Emergence*Climate exp	1.43	1.05	1.34	0.179	0.49
Emergence*Climate common garden	-3.07	1.4	2.17	0.030	0.87
Dorsal darkness	-0.87	0.58	1.5	0.133	0.55
Dorsal darkness*Climate common garden	0.96	0.69	1.37	0.170	0.1
Dorsal darkness*Climare exp	0.95	0.59	1.61	0.108	0.23
Climate exp*Climate common garden	-1.41	1.51	0.92	0.355	0.11
Thermal preference*Climate exp	0.65	0.48	1.35	0.177	0.11
Sex	0.79	0.64	1.22	0.223	0.1
Emergence*Climate exp*Climate common garden	3.02	2.71	1.1	0.271	0.02
Common garden - Adult summer survival - connected populations					
Intercept	1.61	0.88	1.8	0.072	1
Dorsal darkness	1.77	1.01	1.71	0.087	1
Climate exp	-0.1	0.91	0.11	0.911	1
Dorsal darkness*Climate exp	-3.11	1.11	2.75	0.006	1
Body saize	0.53	0.44	1.19	0.236	0.33
Age	-0.7	0.88	0.78	0.434	0.2

Table 3.6 – Summer survival of adults for isolated and connected populations during the common garden experiment. The random structure of models are as follow. Isolated populations: common garden enclosure identity; Connected populations: NA

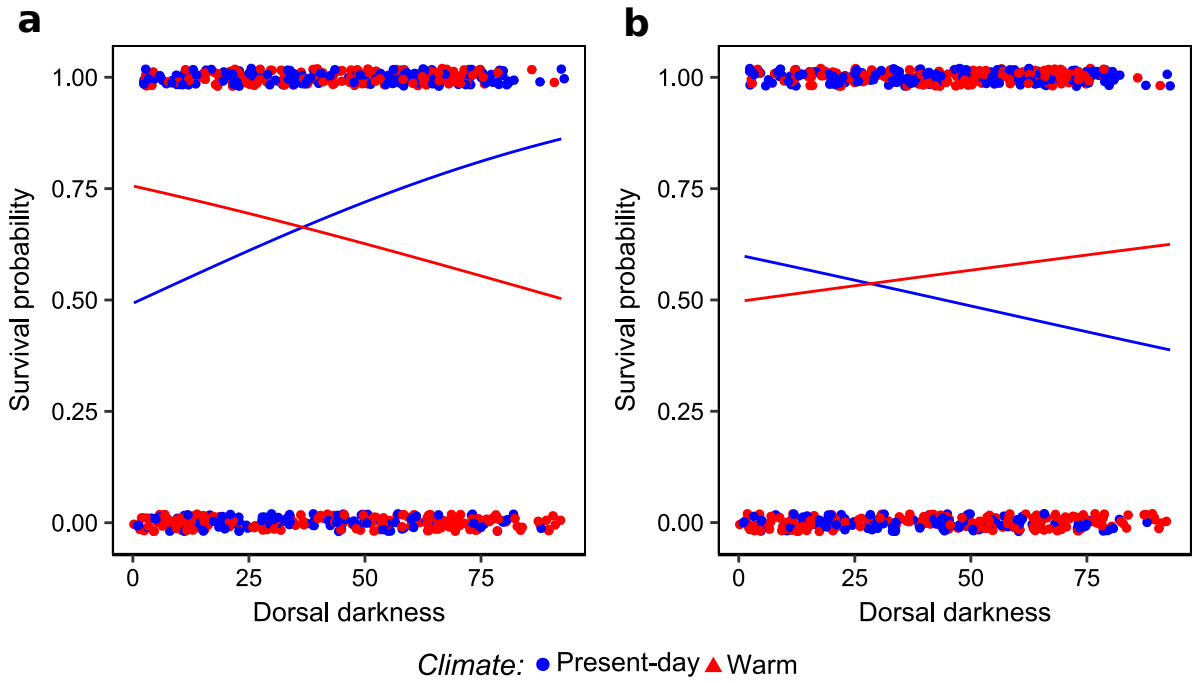

Figure 3.3 – Impact of dorsal darkness on the summer survival of juveniles. Summer survival probability of juveniles as a function of dorsal darkness at birth in isolated (a) and connected (b) populations of present-day (blue) and warm (red) climatic conditions. Dots represent observed data. Lines represent predicts of the model presented in Table 3.4, run on data in isolated (a) and connected (b) populations respectively

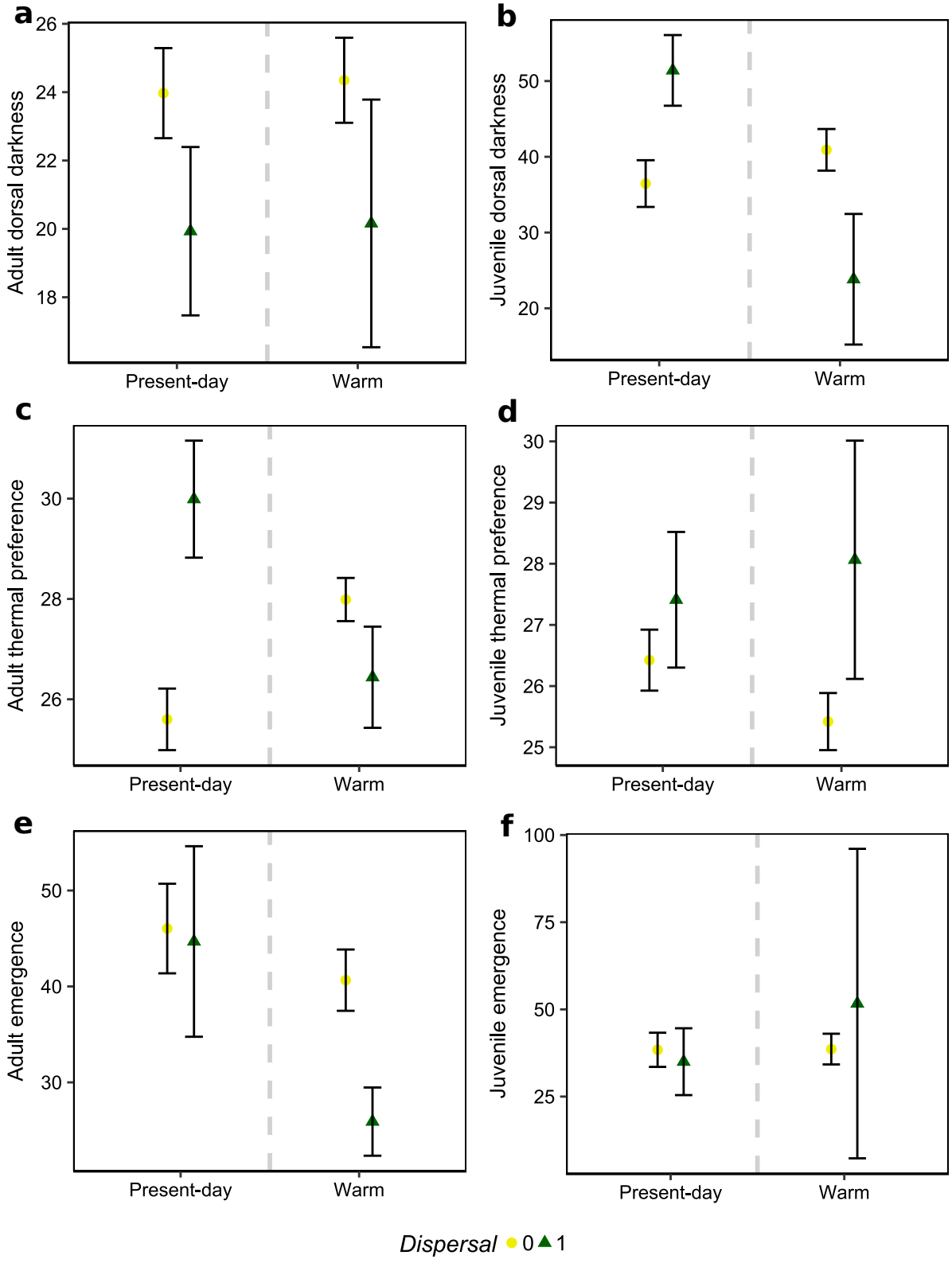

Figure 3.4 – Thermal traits of adult (a,c,e) and juvenile (b,d,e) summer dispersers and residents depending on climatic conditions. Dorsal darkness (a,b), thermal preference (c,d) and daily emergence (e,f) of summer residents (yellow circles) and summer dispersers (green triangles) from population of present-day and warm climatic conditions. Mean ± SE are represented

5 Discussion

Thermal phenotypic distribution of populations was variably influenced by the 3-years long manipulation of climatic conditions and habitat connectivity. Adult individuals became paler in warmer climate than in present-day climate, mostly in isolated populations. This difference in darkness was also observed at birth, but to a lower extent. This phenotypic differentiation among climates mostly resulted from phenotypic plasticity in isolated populations, while it resulted from the joint action of plasticity, selection and dispersal in connected populations. Whereas plasticity increased juvenile dorsal darkness in present-day climate, selection and dispersal acted in synergy to both reduce dorsal darkness in present-day climate and increase it in warm climate. Other thermal traits were weakly influenced by the climatic manipulation, but were affected by habitat connectivity.

The most salient result is that individuals were paler in warmer climate than in present-day climate, mostly in isolated populations. Conversely, thermal preference and emergence were not strongly affected by the climatic conditions. Climate change is known to affect color pattern of organisms (e.g. Galeotti *et al.*, 2009; Zeuss *et al.*, 2014). Melanin-based darkness is involved in many physiological processes such as thermoregulation (Trullas *et al.*, 2007), defense against pathogens (Roulin, 2014; Côte *et al.*, 2018), UV protection (Roulin, 2014) and is linked to behavioral traits (Ducrest *et al.*, 2008). In ectotherms, the thermal melanism hypothesis (Trullas *et al.*, 2007) predicts that darker individuals should be more at risk of overheating under warm conditions than paler individuals, explaining the geographic distribution of organisms along latitudes and altitudes (Castella *et al.*, 2013; Zeuss *et al.*, 2014). Whereas external temperature exceeds thermal limits of ectotherms (Sunday *et al.*, 2014), changes in traits related to the management of thermal conditions such as thermal parameters (optimum, preference and limits), coloration or behavioral profile could reduce mortality risks and extinction (Sinervo *et al.*, 2010). In the case of coloration, we expect climate change to reduce individual darkness in ectotherm to diminish risks of overheating (Zeuss *et al.*, 2014). Our results support this prediction in isolated populations. On the contrary, we did not observe strong ef-

fects of climatic conditions on thermal preference or emergence, suggesting an absence of physiological and behavioral adjustment to climatic conditions. In the common lizard, physiological parameters have been shown to be consistent over space and conditions, highlighting the relative rigidity of thermal physiology to evolution (Van Damme *et al.* (1990), but see Angilletta *et al.* (2002)). Moreover, we measured phenotypes 6 months after the end of the climatic treatment, allowing seasonal readjustment of behaviors. Indeed, early emergence could bring an advantage under warm climate in summer, when temperatures during the warmest hours of the day exceed thermal limits (Sinervo *et al.*, 2010). However, winter and spring temperatures rarely exceed thermal limits, making behavioral adjustments less beneficial.

In isolated populations, adult and juvenile individuals became darker in present-day climate mostly due to phenotypic plasticity. Although statistical support was low in both juveniles and adults, the two stages showed the same plastic trend toward an increase in dorsal darkness in present-day climate relative to warmer climates. Phenotypic plasticity is responsible for the great majority of observed phenotypic changes driven by climate change (Charmantier *et al.*, 2008; Charmantier & Gienapp, 2014; Boutin & Lane, 2014; Urban *et al.*, 2014). Evidence of evolutionary adaptation related to climate change is scarce, also because of the difficulty to demonstrate it (Merilä & Hendry, 2014). Nevertheless, when appropriate methods were used, only a small portion of phenotypic changes were due to evolutionary adaptation (e.g. 13% of the advance in breeding timing of North American red squirrel populations (Réale *et al.*, 2003)). although thermal traits measured in our study were heritable, selection differentials and gradients related to climatic conditions were not strong in isolated populations. It should, however, be noted that in juveniles, selection gradients pointed in the same direction as phenotypic plasticity. On their own, these selection gradients were not strong enough to drive phenotypic changes and differentiation among climates, but may have strengthened effects of climate-induced plasticity.

When populations were connected, evolutionary adaptation and adaptive dispersal, however, offset the influence of phenotypic plasticity. In juveniles, while plasticity slightly

increased dorsal darkness in present-day climate populations, selection during summer favored darker individuals in warm climatic conditions and paler individuals in present-day climatic conditions. As a result, dorsal darkness was not different between climates at the end of the experiment in connected populations (Figure 3.1a). Evolutionary adaptation, dispersal and phenotypic plasticity are predicted to interact to shape population phenotypic change (Crispo, 2008). First, dispersal could constrain evolutionary adaptation through maladaptive gene flow (Lenormand, 2002) but could also promote it by bringing adapted genes, increasing genetic diversity on which selection could act and reducing genetic drift (reviewed in Garant *et al.*, 2007). We demonstrated here that dispersal was adaptive regarding dorsal darkness in juveniles; individuals with the lowest survival expectation dispersed more than individuals with advantageous phenotypes in both climatic conditions. Surprisingly, we observed that dispersal modified the strength and the direction of selection gradients on phenotypic traits in comparison to a situation without dispersal. Matching habitat choice is predicted to promote populations differentiation (Edelaar & Bolnick, 2012; Bolnick & Otto, 2013; Scheiner, 2016; Edelaar *et al.*, 2017), but the spatial sorting of individuals should lessen selective pressures on traits as maladapted individuals escape selection via dispersal. However, dispersal reduces local inbreeding and brings phenotypic and genetic diversity on which the selection could act (Garant *et al.*, 2007). Dispersal is indeed not only driven by the match between phenotype and climate. For instance, morphological characteristics, resource availability and competition also drive dispersal decisions (e.g. Thomas *et al.*, 2001; Cote & Clobert, 2007b; Clobert *et al.*, 2012) and therefore not all the individuals unmatched with local climatic conditions are able to or make the decision to disperse. Some individuals with low dorsal darkness indeed stayed in warmer condition and conversely for darker individuals in present-day climate. As the proportion of adapted individuals increased through dispersal, less adapted individuals might suffer from intraspecific competition with better adapted individuals. As a consequence, selection against these individuals could be stronger in presence of adaptive dispersal than without. However, this hypothesis failed to explain why the direction of the selection gradients between connected and isolated

populations were opposed.

An alternative hypothesis to explain the change in the direction and the strength of selection gradients in presence of dispersal could be linked to the thermal strategies of the individuals. Dorsal darkness could be part of a thermal syndrome in which individuals preferring warmer conditions will be characterized, among many traits, by high dorsal darkness. Darker individuals should warm up faster and could therefore prefer high temperature. These individuals should on average better perform in warm climate than individuals preferring cooler climates, explaining the observed pattern of dispersal. However, periods of extreme temperature should induce a high risk of mortality for darker individuals because of their higher risk to overheat (thermal melanism hypothesis (Trullas *et al.*, 2007)). In connected populations, movement between microclimates may allow these individuals to temporally escape the periods of extreme temperature. In isolated populations, as individuals are constrained into one microclimatic condition, darker individuals could be counter-selected by extreme temperature periods in warm climate, explaining the inverse pattern of selection that we observed between isolated and connected populations. Experiment manipulating extreme climatic events could bring new elements supporting this hypothesis.

Dispersal may also favor phenotypic plasticity over evolutionary adaptation as disperser success depends on their ability to adapt fast to their new habitat (Crispo, 2008). Phenotypic plasticity should therefore be favored in presence of dispersal (Sultan & Spencer, 2002). However, this prediction relies on the fact that dispersal is random. In our case, dispersers arriving in warm or present-day climatic conditions are already adapted to the new condition as the interaction between their phenotype and climate drove their dispersal decisions. Moreover, matching habitat choice could be seen as another way of plastically respond to environmental variations. Indeed, individuals could move rather than plastically adjust their phenotype to the local condition.

Finally, phenotypic plasticity may release selective pressures on phenotypes, reducing evolutionary adaptation (Price *et al.*, 2003; Crispo, 2008; Hendry, 2015). However, previous works suggested that initial phenotypic change due to phenotypic plasticity may

be followed by evolutionary changes in the same direction as phenotypic plasticity (i.e. cogradient variation (Conover & Schultz, 1995; Hendry, 2015)). Conversely, phenotypic plasticity and selection pressures could drive phenotypes in opposite directions (i.e. countergradient variation (Conover & Schultz, 1995)). In the latter case, phenotypic plasticity is assumed to be maladaptive and should be reduced in favor of evolutionary adaptation. In connected populations, we observed such countergradient variation in juvenile dorsal darkness, even if the difference in plasticity was low among climatic conditions. However, we did not observe that plastic changes were maladaptive. Juveniles which became darker in present-day climate the first year were not counter-selected at the adult stage, as no selection pressures acted on dorsal darkness in adults. This result suggested that selection acting on the early stage of life could be reversed later in life. Phenotypic plasticity may allow individuals to cope with local climate despite evolutionary adaptation driving phenotypes in the opposite direction earlier in the life.

The structure of the landscape thus appeared to influence the mechanisms by which population responded to the local climatic conditions. Selective pressures related to climatic conditions might also be offset by selection pressures related to landscape structure. We observed in adults that summer and annual survival were influenced by the interaction between landscape structure and thermal preference. Over one year, selection gradients on thermal preference were positive and negative in present day climate of isolated and connected populations respectively (Table S3.8), underlying the influence of landscape structure on the direction of selection acting on phenotypes. Previous studies demonstrated that landscape structure could select for traits related to dispersal (e.g. emigration probability (Bonte *et al.*, 2006; Schtickzelle *et al.*, 2006), wing shape (Taylor & Merriam, 1995), body size (Thomas *et al.*, 1998; Hill *et al.*, 1999)) or competition (e.g. competitive skills (Knell, 2009)). Multiple morphological, physiological and behavioral traits often correlate to form dispersal syndromes (Clobert *et al.*, 2009, 2012; Cote *et al.*, 2017). Landscape structure could therefore select for multiple traits and correlations that either enhance or hamper dispersal. Selection pressures driven by climatic conditions and landscape structure could act directly or indirectly on the same traits and pull phenotypes

in the same or opposite directions. Fully crossed experiments manipulating both climatic conditions and landscape structure could help better distinguish between the pressures induced by the two treatments. Our experiment, constituted of pairs of present-day and warm climatic treatments, limited our abilities to distinguish between climatic and landscape induced selective pressures on the traits. Isolated and connected pairs of enclosures with homogeneous climatic conditions (both enclosures with the same climatic treatment), associated with our current treatments, could reveal the role of landscape structure on population differentiation, independently of the climatic conditions.

Finally, we did not observe any interaction between the climatic conditions during the main experiment and during the common garden on survival which would have suggested an adaptation (or maldaptation) induced by our treatments. However, some phenotypes performed better in both climates than others, and the favored phenotypes were shaped by our three years of treatments. Darker adult individuals from the 2015-2018 present-day climate of the connected treatment indeed survived better than paler individuals during the common garden experiment, whatever the climatic conditions during the common garden. Conversely, paler adult individuals from the warm climate treatment performed better than darker individuals during the common garden. One explanation could be that these advantaged phenotypes might be more plastic than the others as they were able to better performed in both climatic conditions of the common garden. As phenotypic plasticity can evolve (e.g. Crispo *et al.*, 2010), the conditions experienced by individuals from 2015 to 2018 might have selected for different levels of plasticity. Depending on the climatic treatment, more plastic individuals might have different phenotypic values depending on the selective pressures acting in each condition. Further analyses could link phenotypic values to the level of plasticity and whether degrees of plasticity could influence survival in both climatic conditions.

Altogether, our results highlighted the influence of landscape structure on population adaptation to different climatic conditions. Despite the low population phenotypic differentiation at the end of the experiment, we demonstrated that phenotypic plasticity, evolutionary adaptation and adaptive dispersal influenced population phenotypic compo-

sition under varying climatic conditions. In contrast to previous studies (e.g. Sultan & Spencer, 2002), we found that connectivity among habitats favored climate-dependent selection pressures on phenotypes. Moreover, we showed that dispersal could modify the strength and direction of the selective pressures acting on phenotypes. We believe that the mechanisms involved in population adaptation to different thermal conditions that we highlighted in this study could also play a major role under climate change. We thus advocate future studies to include landscape structure and dispersal mechanisms when studying and predicting species response to climate change.

6 Supplementary materials

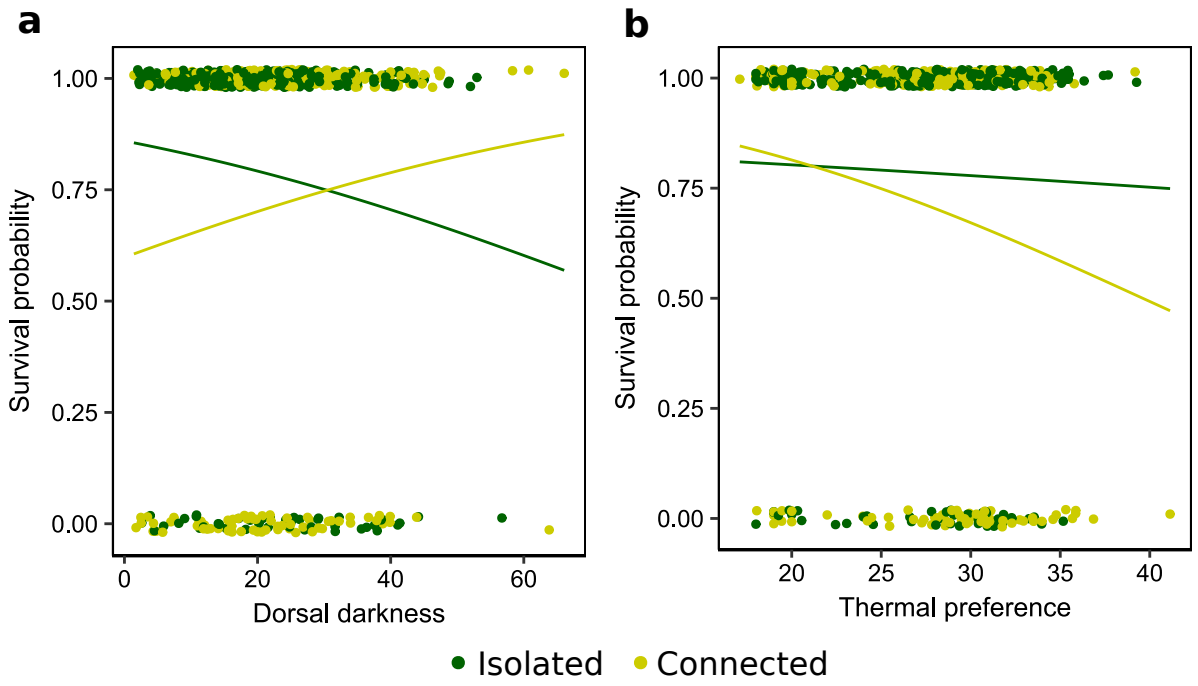

Figure S3.1 – Impact of dorsal darkness (a) and thermal preference (b) on the summer survival of adults in isolated (green) and connected (yellow) populations. Dots represent observed data. Lines represent predicts of the model presented in Table 3.4 for adult summer survival

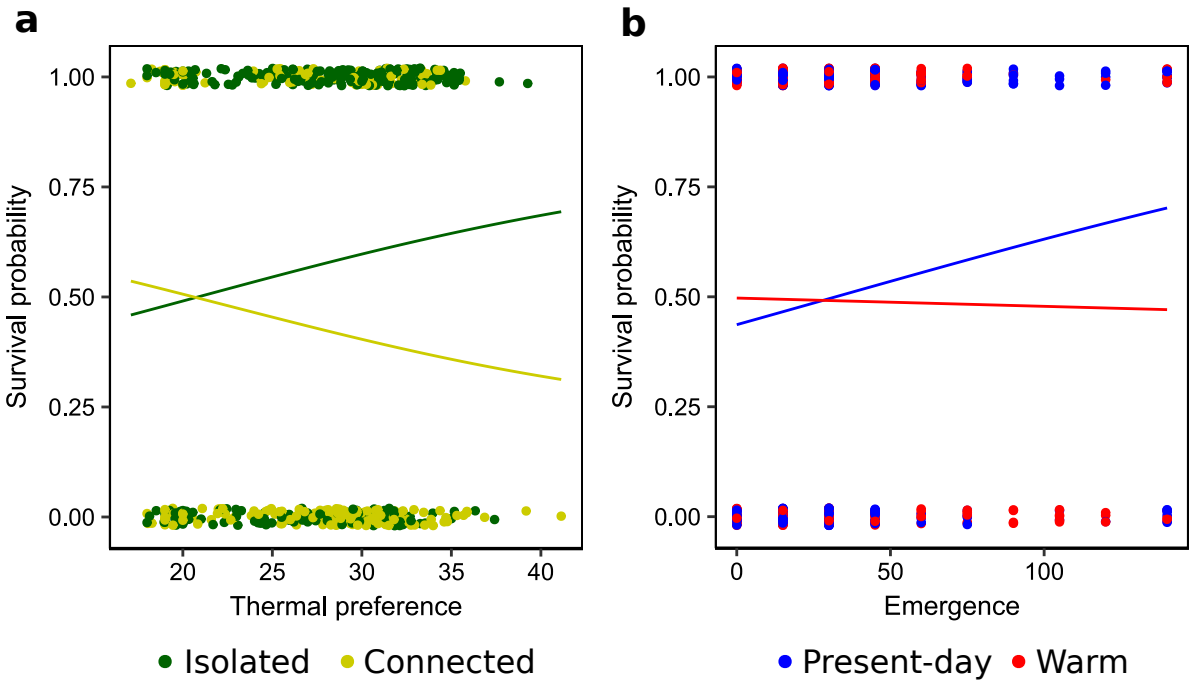

Figure S3.2 – Impact of thermal preference (a) and emergence (b) on the annual survival of adults, in isolated (green) and connected (yellow) populations (thermal preference only) or in present-day (blue) and warm (red) climatic conditions (emergence only). Dots represent observed data. Lines represent predicts of the model presented in Table S3.5 for adult annual survival

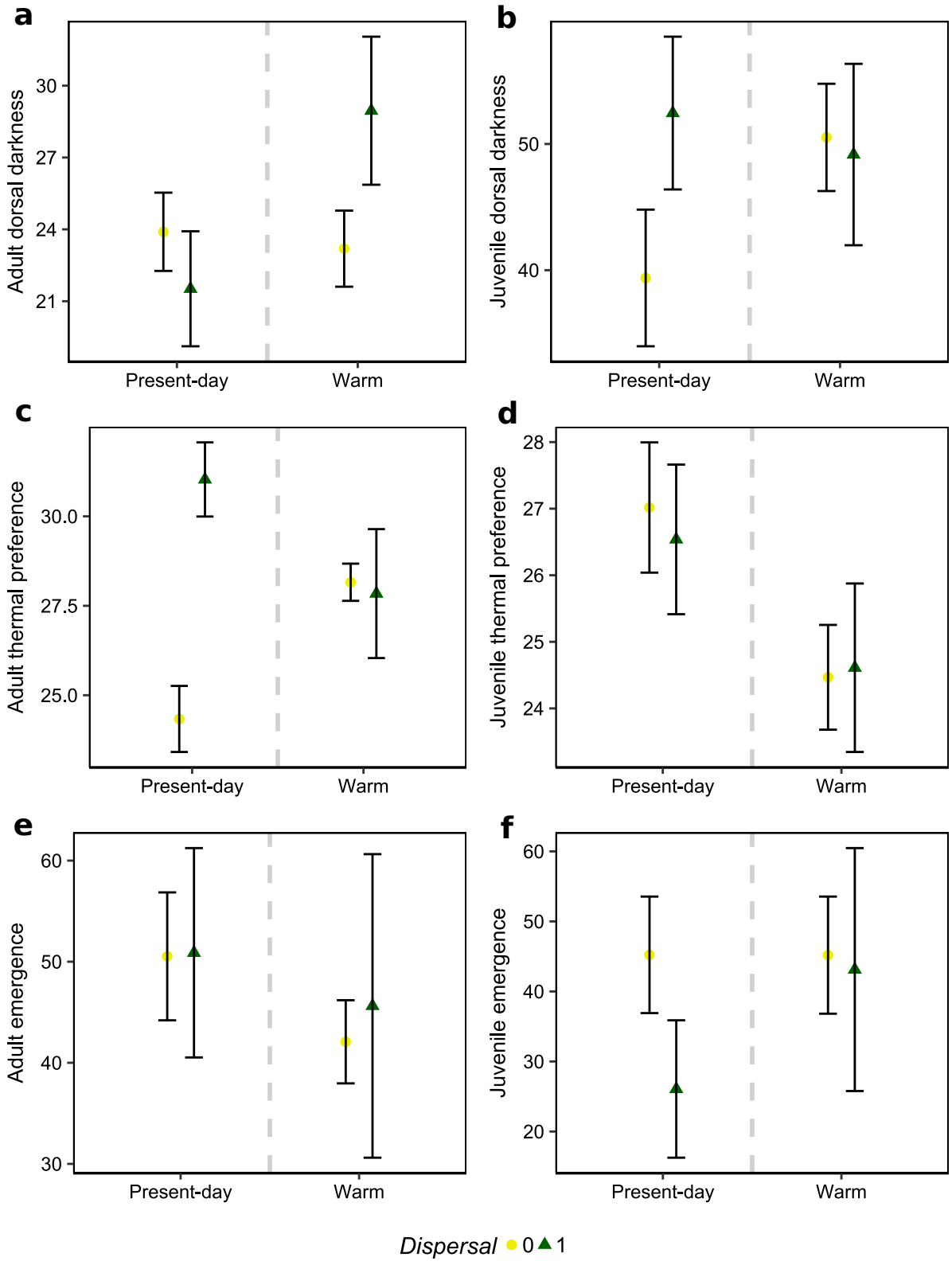

Figure S3.3 – Thermal traits of adult (a,c,e) and juvenile (b,d,e) annual dispersers and residents depending on climatic conditions. Dorsal darkness (a,b), thermal preference (c,d) and daily emergence (e,f) of annual residents (yellow circles) and annual dispersers (green triangles) from population of present-day and warm climatic conditions. Mean ± SE are represented

Variable	Estimate	SE	z-value	P-value	RI
Adult dorsal darkness					
Intercept	30.28	2.11	14.21	<0.001	1
Age	-5.94	3.5	1.69	0.092	1
Sex	5.19	1.85	2.77	0.006	1
Climate	-5.96	1.74	3.4	0.001	1
Body size	-2.3	1.86	1.22	0.221	0.42
Adult thermal preference					
Intercept	25.6	1.11	22.92	<0.001	1
Body size	1.27	0.55	2.29	0.022	1
Sex	1.6	0.76	2.09	0.037	1
Climate	-0.77	0.73	1.05	0.293	0.28
Age	1.29	1.62	0.79	0.432	0.22
Adult emergence					
Climate	0.14	0.26	0.54	0.588	0.31
Emergence room	-0.60	0.46	1.31	0.192	0.4
Body size	-0.20	0.15	1.33	0.183	0.42
Sex	0.54	0.31	1.72	0.086	0.26
Age	0.30	0.26	1.14	0.255	0.25
Juvenile dorsal darkness					
Intercept	55.38	2.56	21.39	<0.001	1
Birth date	4.01	1.2	3.29	0.001	1
Sex	4.09	2.26	1.79	0.074	0.7
Climate	-5.87	2.51	2.3	0.022	1
Body size	0.89	1.21	0.73	0.467	0.21
juvenile thermal preference					
Intercept	27.68	0.9	30.48	<0.001	1
Body size	0.78	0.51	1.51	0.131	0.43
Birth date	0.66	0.61	1.06	0.288	0.25
Climate	1.12	1.24	0.89	0.374	0.21
Sex	-0.5	0.76	0.64	0.522	0.09
Juvenile emergence					
Birth date	0.31	0.13	2.33	0.020	1
Body size	0.34	0.14	2.39	0.017	1
Climate	-0.29	0.29	1.00	0.317	0.28
Sex	0.16	0.25	0.62	0.536	0.21

Table S3.1 – Thermal traits of adults and juveniles after three years of climatic treatments in isolated populations. The random structure of models are as follow. Adult dorsal darkness: NA; Adult thermal preference: enclosure identity and session; Adult emergence: enclosure identity; Juveniles dorsal darkness: NA; Juvenile thermal preference: family identity and arena identity; Juvenile emergence: enclosure identity

Variable	Estimate	SE	z-value	P-value	RI
Adult dorsal darkness					
Intercept	28.31	2.74	10.2	<0.001	1
Age	-7.71	2.8	2.71	0.007	1
Sex	3.04	2.16	1.38	0.168	0.4
Climate	-2.59	2.43	1.04	0.297	0.31
Body size	-1.95	1.98	0.97	0.332	0.15
Adult thermal preference					
Intercept	25.14	1.04	23.8	<0.001	1
Sex	3.32	1.12	2.9	0.004	1
Body size	0.67	0.57	1.15	0.250	0.25
Age	-1.09	1.13	0.95	0.343	0.2
Climate	0.85	1.24	0.67	0.502	0.16
Adult emergence					
Sex	0.44	0.26	1.69	0.090	0.48
Emergence room	0.40	0.28	1.44	0.149	0.27
Climate	-0.30	0.29	1.06	0.291	0.34
Age	-0.12	0.26	0.48	0.631	0.1
Juvenile dorsal darkness					
Intercept	53.22	2.9	17.95	<0.001	1
Body size	-2.85	1.56	1.79	0.073	0.56
Sex	4.53	2.78	1.59	0.111	0.48
Birth date	2.97	2.42	1.2	0.231	0.27
juvenile thermal preference					
Intercept	28.39	0.71	39	<0.001	1
Birth date	-1.03	0.45	2.25	0.025	0.85
Sex	-1.55	0.85	1.77	0.076	0.5
Body size	0.71	0.52	1.34	0.180	0.45
Juvenile emergence					
Birth date	-0.29	0.19	1.53	0.126	0.61
Climate	-0.23	0.49	0.47	0.637	0.31
Sex	0.19	0.31	0.60	0.548	0.13

Table S3.2 – Thermal traits of adults and juveniles after three years of climatic treatments in connected populations. The random structure of models are as follow. Adult dorsal darkness: NA; Adult thermal preference: NA; Adult emergence: enclosure identity; Juveniles dorsal darkness: family identity; Juvenile thermal preference: arena identity; Juvenile emergence: enclosure identity

Variable	Estimate	SE	z-value	P-value	RI
Adult plasticity for dorsal darkness					
Intercept	2.48	1.87	1.32	0.186	1
Age	2.40	1.44	1.66	0.097	0.47
Year2	-2.22	1.94	1.14	0.256	1
Year3	5.14	1.79	2.85	0.004	1
Sex	2.95	1.43	2.04	0.041	1
Climate	-2.61	1.44	1.80	0.072	0.72
Body growth	1.10	0.76	1.44	0.151	0.2
Adult plasticity for thermal preference					
Intercept	-0.16	0.89	0.18	0.855	1
Year2	0.70	1.13	0.62	0.538	1
Year3	-1.97	1.06	1.85	0.064	1
Sex	0.81	0.85	0.95	0.340	0.24
Climate	0.35	0.85	0.40	0.686	0.16
Body growth	0.18	0.45	0.39	0.695	0.16
Adult plasticity for emergence					
Intercept	-0.57	0.25	2.28	0.023	1
Year2	-0.52	0.32	1.61	0.107	1
Year3	1.25	0.30	4.16	<0.001	1
Age	-0.16	0.24	0.64	0.521	0.3
Juvenile plasticity for dorsal darkness					
Intercept	-0.08	0.32	0.25	0.801	1
Body growth	-0.32	0.17	1.81	0.071	0.7
Birth date	-0.52	0.16	3.23	0.001	1
Sex	0.59	0.24	2.42	0.016	1
Climate	-0.52	0.38	1.37	0.172	0.37
Year3	-0.47	0.45	1.03	0.303	0.17
juvenile plasticity for thermal preference					
Intercept	3.59	1.01	3.56	0.001	1
Year3	-4.71	1.37	-3.45	0.001	1
Juvenile plasticity for emergence					
Intercept	-1.18	0.42	2.76	0.006	1
Body growth	-0.78	0.23	3.29	0.001	1
Climate	1.54	0.52	2.94	0.003	1
Birth date	0.12	0.23	0.51	0.611	0.27

Table S3.3 – Plasticity in thermal traits of adults and juveniles after three years of climatic treatments in isolated populations. The best random structure for all model was no random intercept, except for plasticity in dorsal darkness of juveniles where family identity was modeled as random intercept

Variable	Estimate	SE	z-value	P-value	RI
Adult plasticity for dorsal darkness					
Intercept	4.55	2.56	1.76	0.078	1
Age	6.63	3.06	2.14	0.032	1
Year2	-7.34	2.87	2.53	0.012	0.84
Year3	-3.50	3.00	1.15	0.249	0.84
Body growth	-2.21	1.62	1.35	0.177	0.36
Climate	2.26	2.46	0.91	0.365	0.16
Sex	1.78	2.36	0.74	0.458	0.14
Adult plasticity for thermal preference					
Intercept	0.60	0.79	0.75	0.453	1
Climate	-1.04	1.19	0.86	0.391	0.21
Year2	1.37	1.38	0.98	0.328	0.18
Year3	-1.23	1.48	0.82	0.412	0.18
Age	-0.81	1.22	0.65	0.514	0.18
Adult plasticity for emergence					
Intercept	-0.81	0.29	2.80	0.005	1
Climate	0.42	0.36	1.16	0.246	0.37
Age	0.43	0.36	1.18	0.240	0.22
Year2	-0.44	0.42	1.04	0.300	0.19
Year3	0.44	0.45	0.95	0.342	0.19
Sex	0.37	0.35	1.05	0.296	0.19
Body growth	0.14	0.18	0.77	0.441	0.09
Juvenile plasticity for dorsal darkness					
Intercept	1.09	0.4	2.64	0.008	1
Year3	-1.81	0.5	3.52	<0.001	1
Body growth	-0.42	0.19	2.18	0.029	1
Birth date	-0.75	0.21	3.44	0.001	1
Climate	-0.52	0.37	1.37	0.170	0.41
juvenile plasticity for thermal preference					
Intercept	3.2	1.56	2.01	0.044	1
Year3	-5.04	1.66	2.97	0.003	1
Climate	3.3	1.46	2.2	0.028	1
Sex	1.83	1.44	1.24	0.217	0.28
Birth date	-0.64	0.87	0.72	0.472	0.16
Body growth	0.71	0.99	0.7	0.485	0.16
Juvenile plasticity for emergence					
Intercept	-0.12	0.34	0.35	0.727	1
Birth date	0.32	0.28	1.13	0.260	0.29
Sex	0.39	0.49	0.77	0.442	0.14
Body growth	-0.18	0.25	0.73	0.468	0.14
Year3	0.5	0.59	0.82	0.413	0.24

Table S3.4 – Plasticity in thermal traits of adults and juveniles after three years of climatic treatments in connected populations. The best random structure for all model was no random intercept, except for plasticity in dorsal darkness of juveniles where family identity was modeled as random intercept

Variable	Estimate	SE	z-value	P-value	RI
Adult annual survival probability					
Intercept	0.41	0.45	0.91	0.361	1
Age	0.31	0.21	1.50	0.135	0.47
Year2	-0.94	0.26	3.60	<0.001	1
Year3	-0.52	0.30	1.75	0.081	1
Thermal preference	0.26	0.16	1.61	0.108	0.96
Sex	0.68	0.22	3.09	0.002	1
Connectivity	-0.70	0.55	1.27	0.205	0.96
Connectivity*Thermal preference	-0.55	0.24	2.34	0.019	0.96
Emergence	0.27	0.17	1.60	0.109	0.7
Climate	-0.25	0.60	0.42	0.678	0.45
Climate*Emergence	-0.40	0.20	1.96	0.050	0.45
Body size	-0.11	0.11	1.00	0.318	0.15
Climate*Thermal preference	-0.38	0.28	1.38	0.167	0.09
Climate*Connectivity	0.82	0.94	0.87	0.384	0.09
Climate*Connectivity*Thermal preference	0.83	0.40	2.10	0.036	0.09
Dorsal darkness	0.08	0.11	0.71	0.477	0.12
Juvenile annual survival probability					
Intercept	-1.57	0.46	3.42	0.001	1
Thermal preference	-0.20	0.11	1.77	0.077	0.79
Climate	0.83	0.63	1.32	0.187	0.4
Birth date	-0.16	0.13	1.21	0.226	0.22
Emergence	0.12	0.11	1.08	0.281	0.21
Year3	0.22	0.24	0.90	0.368	0.09
Dorsal darkness	-0.03	0.19	0.17	0.864	0.15
Connectivity	-0.04	0.65	0.06	0.955	0.08
Connectivity*Dorsal darkness	0.52	0.25	2.06	0.040	0.08
Sex	0.15	0.22	0.70	0.487	0.1
Body size	0.03	0.13	0.28	0.782	0.03

Table S3.5 – Annual survival of adults and juveniles. The random structure of models are as follow. Adult annual survival probability: enclosure identity; Juvenile annual survival probability: enclosure identity and family identity

		Dorsal darkness		Thermal preference		Emergence	
		$\beta_{avggrad}$	S	$\beta_{avggrad}$	S	$\beta_{avggrad}$	S
Isolated	Present-day	-0.01 [-0.06;0.04]	-0.06	0.01 [-0.04;0.06]	0.04	0.03 [-0.03;0.09]	0.03
	Warm	-0.01 [-0.06;0.04]	-0.03	-0.02 [-0.08;0.03]	-0.08	0.04 [-0.02;0.09]	0.05
Connected	Present-day	0.06 [-0.03;0.15]	0.08	**-0.12 [-0.22;-0.02]**	-0.20	0.03 [-0.06;0.12]	0.08
	Warm	0.02 [-0.06;0.11]	0.02	-0.01 [-0.09;0.07]	0.00	-0.04 [-0.11;0.04]	-0.08

Table S3.6 – Selection gradients ($\beta_{avggrad}$) and differential (S) for dorsal darkness, thermal preference and emergence of adults, calculated on summer survival. Random structure of all models contained enclosure identity

		Dorsal darkness		Thermal preference		Emergence	
		$\beta_{avggrad}$	S	$\beta_{avggrad}$	S	$\beta_{avggrad}$	S
Isolated	Present-day	0.04 [-0.08;0.16]	0.06	-0.05 [-0.12;0.02]	-0.12	-0.05 [-0.12;0.02]	-0.05
	Warm	-0.04 [-0.16;0.08]	-0.02	0.00 [-0.07;0.06]	-0.05	-0.01 [-0.08;0.05]	-0.11
Connected	Present-day	**-0.14 [-0.28;-0.01]**	-0.11	-0.07 [-0.16;0.02]	-0.15	0.01 [-0.08;0.09]	-0.01
	Warm	**0.17 [0.02;0.31]**	0.13	0.05 [-0.03;0.14]	-0.03	0.00 [-0.07;0.08]	-0.02

Table S3.7 – Selection gradients ($\beta_{avggrad}$) and differential (S) for dorsal darkness, thermal preference and emergence of juveniles, calculated on summer survival. Random structure of all models contained enclosure identity and family identity

		Dorsal darkness		Thermal preference		Emergence	
		$\beta_{avggrad}$	S	$\beta_{avggrad}$	S	$\beta_{avggrad}$	S
Isolated	Present-day	-0.01 [-0.08;0.06]	-0.05	**0.06 [0;0.13]**	0.16	0.07 [-0.01;0.15]	0.10
	Warm	0.02 [-0.06;0.1]	0.02	0.00 [-0.08;0.08]	0.00	0.02 [-0.05;0.1]	0.05
Connected	Present-day	0.04 [-0.04;0.13]	0.37	**-0.11 [-0.2;-0.01]**	-0.17	0.04 [-0.04;0.12]	-0.02
	Warm	0.00 [-0.09;0.1]	0.00	0.01 [-0.09;0.11]	0.04	0.02 [-0.08;0.11]	0.01

Table S3.8 – Selection gradients ($\beta_{avggrad}$) and differential (S) for dorsal darkness, thermal preference and emergence of adults, calculated on annual survival. Random structure of all models contained enclosure identity

		Dorsal darkness		Thermal preference		Emergence	
		$\beta_{avggrad}$	S	$\beta_{avggrad}$	S	$\beta_{avggrad}$	S
Isolated	Present-day	-0.05 [-0.17;0.07]	-0.06	-0.02 [-0.08;0.03]	-0.25	0.03 [-0.02;0.08]	0.21
	Warm	-0.02 [-0.14;0.1]	-0.01	-0.05 [-0.11;0.02]	-0.14	-0.01 [-0.08;0.06]	-0.14
Connected	Present-day	-0.10 [-0.24;0.05]	-0.15	-0.04 [-0.13;0.04]	-0.14	0.02 [-0.05;0.1]	0.12
	Warm	**0.12 [0.01;0.24]**	0.37	-0.03 [-0.09;0.04]	-0.25	0.04 [-0.02;0.1]	0.02

Table S3.9 – Selection gradients ($\beta_{avggrad}$) and differential (S) for dorsal darkness, thermal preference and emergence of juveniles, calculated on annual survival. Random structure of all models contained enclosure identity and family identity

Variable	Mean (SE)	V_A	V_M	V_E	V_R	h^2	ΔDIC	CV_A
Natal thermal preference	26.51 (0.1)	3.56 (0.06)	2.34 (0.02)	1.03 (0.01)	13.25 (0.04)	0.18 [0.05 – 0.35]	69.1	7
Natal dorsal darkness	47.19 (0.7)	56.51 (0.56)	81.05 (0.52)	18.64 (0.23)	66.80 (0.38)	0.25 [0.10 – 0.41]	162.7	16
Natal emergence	42.00 (1.4)	402.14 (6.76)	155.90 (1.96)	72.62 (0.98)	1199.78 (5.36)	0.22 [0.05 – 0.46]	59.3	48

Table S3.10 – Heritability of natal dorsal darkness, thermal preference and log-transformed emergence. Components of additive genetic variance (V_A), of maternal variance (V_M), of parents' environmental variance and residual variance (V_R) are estimated from univariate models with year as fixed effects and animal, mother ID and parents' mesocosm per year ID random effects. We further provided mean trait values (± SE), heritability (mean h^2 and 95% CI), coefficients of additive genetic variation (CV_A) and differences in DIC between a model with and a model without an animal effect

Variable	Estimate	SE	z-value	P-value	RI
Adult annual dispersal					
Intercept	-1.02	0.41	2.49	0.013	1
Thermal preference	1.28	0.40	3.15	0.002	1
Climate	-0.89	0.54	1.62	0.106	1
Climate*Thermal preference	-1.39	0.63	2.20	0.028	1
Emergence	0.32	0.26	1.21	0.225	0.23
Body size	0.30	0.29	1.02	0.306	0.19
Sex	0.33	0.57	0.57	0.571	0.13
Dorsal darkness	0.14	0.26	0.53	0.593	0.13
Juvenile annual dispersal					
Intercept	2.49	0.94	2.66	0.008	1
Climate	-1.63	0.71	-2.29	0.022	1
Dorsal darkness	2.40	0.69	3.49	0.000	1
Year3	-4.90	1.45	-3.39	0.001	1
Birth date	-1.13	0.51	-2.21	0.027	1
Climate*Dorsal darkness	-1.43	0.70	-2.06	0.040	1

Table S3.11 – Annual dispersal probability of adults and juveniles. The random structure of models are as follow. Adult annual dispersal: NA; Juvenile annual dispersal: NA

Variable	Estimate	SE	z-value	P-value	RI
Common garden - Adult summer survival					
Intercept	1.73	0.53	3.24	0.001	1
Body size	0.23	0.2	1.18	0.237	0.19
Climate exp	-0.28	0.41	0.67	0.503	0.12
Age	-0.2	0.39	0.52	0.603	0.11
Connectivity exp	0.21	0.42	0.51	0.613	0.11
Sex	0.17	0.39	0.44	0.658	0.11
Climate common garden	0.36	0.92	0.39	0.699	0.1
Common garden - Juvenile summer survival					
Intercept	1.1	0.51	2.15	0.032	1
Climate common garden	0.8	0.87	0.9	0.366	0.27
Birth date	-0.18	0.21	0.86	0.389	0.25

Table S3.12 – Summer survival of adults and juveniles during the common garden experiment. The random structure of models are as follow. Adult summer survival: common garden enclosure identity; Juvenile summer survival: common garden enclosure identity

4 Matching habitat choice promotes species persistence under climate change

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1 Abstract

Species may survive under contemporary climate change by either shifting their range or adapting locally to the warmer conditions. Theoretical and empirical studies recently underlined that dispersal, the central mechanism behind these responses, may depend on the match between an individuals' phenotype and local environment. Such matching habitat choice is expected to induce an adaptive gene flow, but it now remains to be studied whether this local process could promote species' responses to climate change. Here, we investigate this by developing an individual-based model including either random dispersal or temperature-dependent matching habitat choice. We monitored population composition and distribution through space and time under climate change. Relative to random dispersal, matching habitat choice induced an adaptive gene flow that lessened spatial range loss during climate warming by improving populations' viability within the range (i.e. limiting range fragmentation) and by facilitating colonization of new habitats at the cold margin. The model even predicted range contraction under random dispersal but range expansion under optimal matching habitat choice. These benefits of matching habitat choice for population persistence mostly resulted from adaptive immigration decision and were greater for populations with larger dispersal distance and higher emigration probability. We also found that environmental stochasticity resulted in suboptimal matching habitat choice, decreasing the benefits of this dispersal mode under climate change. However population persistence was still better under suboptimal matching habitat choice than under random dispersal. Our results highlight the urgent need to implement more realistic mechanisms of dispersal such as matching habitat choice into models predicting the impacts of ongoing climate change on biodiversity.

2 Introduction

Contemporary climate change threatens biodiversity worldwide by impacting species persistence and distribution (Parmesan, 2006; Selwood *et al.*, 2015; Urban, 2015). Species may persist under climate change through two main non-exclusive responses: by tracking suitable climatic conditions across space (geographical range shift, e.g. Hill *et al.* (2011), Chen *et al.* (2011)) or by adapting to the new local climatic conditions without shifting their geographic range (populations' phenotypic shift, e.g. (Boutin & Lane, 2014; Merilä & Hendry, 2014). Both responses are strongly influenced by dispersal (i.e. movement from the natal site to the first breeding site, or between successive breeding locations (Howard, 1960)). Dispersal allows the colonization of new habitats made available by climate change and induces a gene flow affecting population's phenotypic composition. Assuming that individuals disperse with a constant probability and settle into randomly chosen habitats, gene flow is predicted to swamp local adaptation by bringing non-adapted alleles into populations (Lenormand, 2002), which could compromise persistence under climate change (Pease *et al.*, 1989; Polechová *et al.*, 2009).

However, dispersal is increasingly recognized to be a non-random process (Bowler & Benton, 2005; Edelaar *et al.*, 2008; Clobert *et al.*, 2009; Edelaar & Bolnick, 2012; Travis *et al.*, 2012; Lowe & McPeek, 2014). The different stages of this process (i.e. departure, transience and settlement) are influenced by individual phenotype, local context and often their match (i.e. matching habitat choice). Variation in the phenotype of individuals may imply variation of fitness in specific environments which should select for inter-individual differences in emigration and immigration decisions according to their fit to local environmental conditions (Edelaar *et al.*, 2008). Individuals are expected to move from habitats where they expect a low fitness and to settle in habitats where they expect a higher fitness, making dispersal an adaptive process.

Matching habitat choice has been demonstrated in various species (e.g. insects (Karpestam *et al.*, 2012), fishes (Bolnick *et al.*, 2009), birds (Dreiss *et al.*, 2012; Camacho *et al.*, 2016; Benkman, 2017), reptiles (Cote & Clobert, 2007a; Cote *et al.*, 2008)), for dif-

ferent phenotypic traits matching different environmental conditions. For example, in three-spine sticklebacks (*Gasterosteus aculeatus*), a mark-transplant-recapture experiment showed that dispersers' preferences for lake and stream habitats depended on lake-like and stream-like morphological attributes (Bolnick *et al.*, 2009). Under stable environmental conditions, matching habitat choice is predicted to promote adaptive gene flow compared to fitness independent dispersal (Holt, 1987; Jaenike & Holt, 1991; Ruxton & Rohani, 1999; Armsworth & Roughgarden, 2005b, 2008; Bolnick & Otto, 2013; Scheiner, 2016). Such adaptive gene flow acts as one of the main factors favoring population adaptation and differentiation on small spatio-temporal scales (Edelaar & Bolnick, 2012; Bolnick & Otto, 2013; Scheiner, 2016; Edelaar *et al.*, 2017). Despite the influence of matching habitat choice on local eco-evolutionary dynamics, there remains scope for exploring whether this individual behavioral process acting at a small spatial scale can influence species' responses to environmental conditions at larger spatial scales.

Under variable environmental conditions, matching habitat choice and ensuing adaptive gene flow may locally promote an efficient shift in mean populations' phenotypes and therefore may influence species' responses to changing conditions such as ongoing climate change. For example, in ectotherm species, physiology directly depends on external temperature and individuals are characterized by a thermal phenotype (i.e. thermal optimum and tolerance) that links their physiology and performance to temperature (Huey & Stevenson, 1979). This thermal phenotype can vary within species and populations (Artacho *et al.*, 2013; Goulet *et al.*, 2017). Thereby, individual thermal optimum may shape individuals' movements across a landscape through the filter of phenotypic adaptations to varying temperature (Bestion *et al.*, 2015a). As climate warming is expected to increase local mismatch between individual thermal optimum and local temperature, matching habitat choice may make movements towards more suitable climatic conditions easier and promote an efficient shift of species geographic distribution (Edelaar & Bolnick, 2012). However to our knowledge, this verbal prediction remains untested and the underlying mechanisms by which matching habitat choice may influence species' responses to climate change are still poorly understood.

Here we investigate the influence of matching habitat choice on species' responses to climate change and more precisely how very local mechanisms, here non-random individual movements, could influence species' global response to environmental change. We used an individual-based model to tackle this question to allow precise integration of such a complex process into the model. Thus, we developed a mechanistic individual-based model representing a virtual species, inspired by the biology of ectotherm species, distributed along a thermal gradient. We modeled two dispersal modes: random dispersal and matching habitat choice. We simulated different rates of climate change and followed populations' genetic composition through space and time. After quantifying the adaptiveness of gene flow under both dispersal modes, we evaluated the influence of adaptive dispersal on extinction risk at the edges of and within the spatial range, on the proportion of the geographical range within which the species goes extinct during climate change and on the time to species extinction.

3 Materials and methods

All parameters used in the model are summarized in Table 4.1.

3.1 Environment

Individuals were distributed on a two dimensional landscape (i.e. grid map) constituting 1700 lines (latitudes) and 15 columns (longitudes) built as a tube to avoid edge effects. A thermal gradient representing mean annual temperatures with 0.01°C increment per space unit occurred along the latitudinal axis. Before climate change, temperature ranged from 19°C to 36°C, preventing any individual from surviving at the edges of the latitudinal axis according to their initial genotypic/phenotypic values (Table 1) and therefore avoiding edge effects on the latitudinal axis. Temperature along the longitudinal axis was constant (no environmental stochasticity, though see robustness section). We assumed that all map cells could sustain a population with constant carrying capacity K through space and time (i.e. continuous landscape with no unsuitable habitats). We simulated two

Parameters	**Main simulations**	**Extra simulations**
Fecundity	2	1 and 3
Mean juvenile survival probability	0.12	0.25
Mean adult survival probability	0.5	0.6
Carrying capacity K	100	50 and 150
Juvenile emigration probability range for matching habitat choice (ε_{basal} and ε_{max} for juveniles)	0.3-0.5	0.2–0.4 and 0.4–0.6
Adult emigration probability range for matching habitat choice (ε_{basal} and ε_{max} for adults)	0.15–0.35	0.05–0.25 and 0.25 – 0.45
Juvenile emigration probability for random dispersal	0.3	0.2, 0.4, 0.5 and 0.6
Adult emigration probability for random dispersal	0.15	0.05, 0.25, 0.35 and 0.45
Dispersal distance	2, 3, 4, 5 and 6	3, 4 and 5
Mutation probability	10^{-5}	10^{-7}
Loci number	25	25
Initial allele range	29–33°C	29–33°C
Time of stable climate	600	800
Warming time	600	600
Level of climate change	1 and 2°C/100 years	1 and 2°C/100 years
Environmental stochasticity	0	0.01, 0.1, 1
Thermal gradient	0.01°C/latitude	0.01°C/latitude
Number of latitude on the map	1700	1700
Number of longitude on the map	15	15
Replicate	50	20

Table 4.1 – Summary of the model parameters and their values in the main simulations and in extra simulations performed for robustness analyses.

levels of climate change (1°C or 2°C of warming over 100 years) by uniformly increasing temperature at each location through time.

3.2 Population dynamics and genetics

We modeled a sexual species with two life stages (juveniles and adults). Each individual was characterized by a thermal phenotype represented as a Gaussian function of survival dependency to temperature with constant variance among individuals and mean corresponding to individual thermal optimum (Equation (4.1))

$$S(T) = \exp(\frac{(T - T_{opt})^2}{2\sigma^2}) \tag{4.1}$$

with $S(T)$ being the survival probability, T the local temperature, σ^2 the gaussian variance and $Topt$ the thermal optimum. This optimum was genetically determined by 25 additive independent diploid loci with values taken from real numbers (i.e. genotypic values corresponding to phenotypic ones; the thermal optimum of each individual was thus obtained by averaging all allele values of its genotype). As a complex continuous trait, we considered that the thermal optimum was genetically determined by many independent loci with infinitesimal effects on the phenotypic trait. We arbitrarily chose to fix this number at 25. We assume no environmental effect (i.e. no phenotypic plasticity). In each population at each time step (one time step corresponds to one year), individuals could disperse, then reproduce (adults only) and survive or die (Figure S4.1). Reproduction was independent of temperature. Each adult female produced a number of offspring taken from a Poisson distribution, with a mean fecundity of 2. Reproducing males were randomly chosen from the same patch. For each transmitted allele, mutation occurred with a probability of 10^{-5} (Table 4.1). The new allele was taken from a Gaussian distribution centered on the mean parental allele value and of arbitrary variance 1.11. With such variance, 95% of new alleles were in a ± 1 interval around the parental value. The sex of offspring was randomly chosen, resulting in a population sex-ratio of 1:1 at birth.

At the end of each time step, individuals died or survived. If juveniles survived they

became adults and the adult stage lasted until individuals died. Survival probability depended on the match between thermal phenotype and external temperature in juveniles and adults (i.e. Gaussian function of temperature (Equation (4.1)); Figure S4.1). For each phenotype, the Gaussian function was scaled such that within the temperature range of $\pm 2.4°C$ around the optimal temperature (which corresponds to the temperature range in which the non-scaled survival probability was always higher than 0.05), the mean survival probability was equal to 0.12 for juveniles and 0.5 for adults (Table 4.1). As observed in many species (e.g. Martin (1995) (birds), Pike *et al.* (2008)(reptiles), Gaillard & Yoccoz (2003) (mammals)), we considered the survival probability to be lower in juveniles than in adults. Survival was also density dependent: when current population size in a patch, N, exceeded carrying capacity K, each individual was killed with a probability $1 - \frac{N}{K}$, so that the population size did not exceed on average the carrying capacity after the survival event. The density-dependent survival event occurred after the phenotype-dependent survival event.

We implemented two different dispersal modes, random dispersal and matching habitat choice. In the case of matching habitat choice, the departure probability of each individual depended on its expected lifetime reproductive success (LRS) (Le Galliard *et al.*, 2008) and was exclusively driven by local thermal adaptation, that is the match between individual thermal phenotype and local temperature (i.e. survival probability without density dependence called hereafter thermal survival probability; Figure S4.1). The lifetime reproductive success was calculated without density dependence for one year (i.e. the adult stage) for adults and for two years (i.e. the juveniles and the adult stage) for juveniles (Equation (4.2)).

$$\begin{aligned} LRS_{adult} &= Fecundity + Surv_T * Fecundity \\ LRS_{juvenile} &= Surv_T * LRS_{adult} \end{aligned} \tag{4.2}$$

with LRS_{adult} and $LRS_{juvenile}$ being the lifetime reproductive success of adults and juveniles respectively and $Surv_T$ being the thermal survival probability. As we did not

know the number of years an individual could live, we assumed the same reproductive success over the years for adults. LRS_{adult} was therefore calculated for one year as calculating LRS over a longer period of time will not change its value. Emigration probability for each individual was calculated as $1 - LRS$ and scaled to mimic realistic dispersal probabilities observed in nature. We considered higher dispersal in juveniles than in adults, as observed in species were natal dispersal is dominant over breeding dispersal (e.g. Greenwood & Harvey (1982). Dispersal probability thus varied from 0.3 to 0.5 for juveniles and from 0.15 to 0.35 for adults (Table4.1). The detailed formula was as follow (Equation (4.3)):

$$\varepsilon = \varepsilon_{basal} + (\varepsilon_{max} - \varepsilon_{basal}) * (1 - (LRS/LRS_{max})) \tag{4.3}$$

with ε the dispersal probability, ε_{basal} the lower dispersal bound (e.g. 0.3 in juveniles), ε_{max} the upper dispersal bound (e.g. 0.5 for juveniles), LRS the lifetime reproductive success (Equation (4.2)) and LRS_{max} the maximum LRS obtained when individual thermal optimum perfectly matches local temperature. Dispersers could visit all habitats on the perimeter of a circle centered on the middle of the departure habitat and of radius exactly equal to the dispersal distance and settled in the habitat that maximized their lifetime reproductive success (Figure S4.1). We assumed that dispersers had access to every habitat on that perimeter, including those where only a corner was on the circle's perimeter (i.e. as each habitat corresponded to a square on the map). Habitats at a distance from the departure habitat lower than the dispersal distance cannot be chosen to settle. Within a simulation, dispersal distance was fixed and all individuals thus dispersed at the same distance from their departure habitat. When more than one habitat maximized their lifetime reproductive success, dispersers settled randomly in one of these habitats (Figure S4.2).

In case of random dispersal, individuals dispersed with a constant probability (0.3 for juveniles and 0.15 for adults; Table 4.1). As the effective dispersal rate in the case of matching habitat choice was not constant over space and time, we set the random dispersal probability to be equal to the lower dispersal probability ε_{basal} from the matching

habitat choice scenario. We also ran simulations with random dispersal probability set to the upper dispersal probability ε_{max} from the matching habitat choice mode, allowing us to compare random dispersal with matching habitat choice scenarios for comparable dispersal probability (see robustness section). Dispersers visited all habitats on the perimeter of a circle centered on the middle of the departure habitat and of radius equal to the dispersal distance and settled in a randomly chosen habitat among these visited habitats (Figure S4.2). Again, all individuals thus dispersed at the same distance from their departure habitat. It allowed us to compared results obtained under matching habitat choice to the random dispersal mode without having differences in the effective dispersal distances between dispersal modes. The results we obtained by comparing simulations under both dispersal modes were thus only due to the direct effect of habitat choice in emigration and immigration decisions. The dispersal distance was fixed within simulations; we ran simulations with five dispersal distances (2, 3, 4, 5, 6 units on the landscape per dispersal event corresponding to a change of 0.02, 0.03, 0.04, 0.05 and 0.06°C on the thermal gradient).

To disentangle the influence of emigration from immigration in the matching habitat choice mode, we ran simulations with adaptive emigration only (dispersal probability depending on the match between phenotype and habitat of origin but random settlement decision) and adaptive immigration only (fixed dispersal probability but settlement decision depending on the match between phenotype and habitat visited).

3.3 Simulations

At the beginning of simulations, we built a landscape and implemented a population of size corresponding to the carrying capacity at each location of that landscape (i.e. the entire landscape was inhabited at carrying capacity, fixed at 100 individuals at every location of the map). For each individual, the allele values of the 25 loci determining the thermal optimum were taken from a uniform distribution between 29 and 33°C (Table 4.1). The initial sex-ratio was 1 : 1 and the proportions of juveniles and adults were 0.5 each. The system evolved under stable climate for 600 years. As mutations

brought new alleles into the populations, the range was not stabilized and the species would invade the landscape after a sufficient time under stable climate. We choose 600 years of stable climate before simulated climate change because it matched the minimum time needed for all phenotypes expressed from the initial distribution of genotypes (i.e. uniform distribution between 29°C and 33°C) to be distributed on the landscape among all parameter values we tested. In the parameter set that led to the widest range size, the individuals were distributed between latitude 100 and latitude 900 corresponding to a range of temperature from 27 to 35°C on the grid. We also ran simulations with 800 years of stable climate and did not observe any difference in the results we obtained from those obtained with 600 years of stable climate (Figure S4.18,S4.19,S4.20,S4.21). Then we simulated climate change for 600 years with two levels of climate change (1°C and 2°C of warming over 100 years) by uniformly increasing temperature at each location through time. The model was coded in C++ using the GNU Scientific Library for random numbers generation (Galassi *et al.*, 2009) and outputs were analyzed using R3.3.1 (R Core Team, 2017).

We show the results for 20 sets of parameters values (2 dispersal modes * 2 levels of climate change * 5 dispersal distances), each one replicated 50 times. Simulations with adaptive emigration only and adaptive immigration only were replicated 20 times. Extra simulations for the robustness of results against various parameters of the model were replicated 20 times. The number of replication was sufficient to obtain very low standard error in our results as running simulations with 40 replicates gave the same results.

3.4 Outputs

At the end of each time step, we calculated the mean thermal survival probability (i.e. the mean survival probability of all individuals without density dependence) through time for residents, immigrants and emigrants of each population across the range. We then calculated gene flow adaptation as the difference between immigrants' relative adaptation (i.e. difference between the mean thermal survival probability of immigrants and the mean thermal survival probability of residents of each population) and emigrants' relative

adaptation (i.e. difference between the mean thermal survival probability of emigrants and the mean thermal survival probability of residents of each population).

The proportion of range loss was computed as $1 - \frac{N_t}{N_0}$ with N_t the number of non-empty latitudes (i.e. one individual at least was present at the given latitude) at time t and N_0 the number of non-empty latitudes at time 0 (i.e. just before the start of the climate change). The extinction time was computed as the number of years of climate change needed for all populations to go extinct. When extinction did not occur during the simulation time (600 years), extinction time was arbitrarily recorded as 600 years. Range contraction was computed as $1 - \frac{R_t}{R_0}$ with R_t being the range size (difference between extreme occupied latitudes) at time t. Range fragmentation was computed as $\frac{R_t - N_t}{R_t}$. Finally, the local mean thermal fitness load was computed at each location and time as one minus the mean thermal survival probability of residents.

3.5 Robustness

To test for the robustness of our results regarding the influence of major demographic parameters known to impact species' responses to climate change, we ran additional simulations for different parameter values of mean survival probability, fecundity, carrying capacity and dispersal probability. We varied the basal dispersal probability ε_{basal} from 0.2 to 0.4 for juveniles and from 0.05 to 0.25 for adults. For simplicity, the range of variation of the emigration probability for matching habitat choice was fixed at 0.2 in all simulations. We added extra simulations of random dispersal with emigration probability of 0.5 and 0.6 for juveniles and 0.35 and 0.45 for adults, corresponding to the maximal emigration probability at which individuals could disperse in the matching habitat choice simulations. This allowed us to compare results obtained under matching habitat choice and random dispersal with similar dispersal rate. The different values for each parameter are provided in Table 4.1.

We also tested the influence of spatio-temporal environmental stochasticity on our results. Environmental stochasticity could influence species' responses to climate change because it should reduce the adaptiveness of the immigration decision in matching habitat

choice mode (a right choice at time t could be wrong at time $t+1$). At each time step (i.e. one year), the temperature of each cell of the map was calculated as the current mean temperature of the latitude + γ, with γ being a temperature randomly taken from a uniform distribution centered on 0 and of variance determined by the level of environmental stochasticity. The higher the environmental stochasticity is, the farther the temperature of a habitat can be from the mean temperature of the latitude. An individual that chooses a habitat that fits its phenotype at time t could therefore be maladapted the year after as the temperature changes stochastically. We ran simulations with environmental stochasticity corresponding to the temperature difference between 2 latitudes (0.01°C), 10 latitudes (0.1°C) and 100 latitudes (1°C). Parameters values are summarized in Table 4.1.

We also considered density dependence in matching habitat choice to test for the influence of the other factors involved in dispersal decisions. We thus included the density-dependent survival term in the lifetime reproductive success of both juveniles and adults (Equation (4.4)).

$$\begin{aligned} LRS_{adult.density} &= Fecundity + Surv_T * Surv_D * Fecundity \\ LRS_{juvenile.density} &= Surv_T * LRS_{adult} \end{aligned} \tag{4.4}$$

with $Surv_T$ being the thermal survival probability and $Surv_D$ being the density dependent survival probability.

Finally, we ran simulations with low mutation rate (10^{-7} per locus; Table 4.1) to study the influence of mutations on the velocity of range shift.

4 Results

We observed that matching habitat choice induced an adaptive gene flow under climate change (Figure 4.1A, Figure S4.3A, S4.4A) while gene flow was never adaptive in the random dispersal mode. Such adaptive gene flow resulted in a higher thermal survival probability (i.e. survival probability without density dependence) of all individuals in

the case of matching habitat choice than in the case of random dispersal (Figure 4.1B, Figure S4.3B, S4.4B). In the matching habitat choice mode, we observed that thermal survival probability was generally higher for immigrants than for residents and emigrants excepted at time 0 where thermal survival probability was maximal for all individuals (Figure 4.1B and Figure S4.3B, S4.4B). In some cases, we also observed that residents' thermal survival probability was higher than emigrants' thermal survival probability (for example: Figure 4.1A; Dispersal distance: 2 space units; Time: 200 years). In the matching habitat choice mode, immigrants were therefore better adapted than residents and emigrants were therefore less adapted that residents, resulting in an adaptive gene flow. Conversely, we did not observe any difference in thermal survival probability between residents, immigrants and residents from the random dispersal modes (Figure 4.1B and Figure S4.3B, S4.4B), preventing gene flow from being adaptive.

The adaptive gene flow due to matching habitat choice decreased the probability that populations go extinct under both climate change scenarios tested and, when extinction occurred, matching habitat choice delayed it (Figure 4.2C, D). The spatial range loss was always lower with matching habitat choice than when individuals moved randomly (Figure 4.2A, B). The difference in spatial range loss between dispersal modes could be large for some sets of parameters. For example, while climate warming led to an extensive loss of 50% of the species range under a certain set of parameters of the random dispersal mode, in the matching habitat choice mode the same set of parameters led to an expansion of the spatial range (e.g. Figure 4.2A, dispersal distance: 3 space units). The spatial range loss was above 25% for most of the parameter values in the random dispersal mode (9 out of 10 sets of parameters), while it only surpassed 25% in three out of 10 sets of parameters in the matching habitat choice mode (Figure 4.2A, B). Furthermore, matching habitat choice almost always allowed species persistence for longer periods of time than random dispersal with a time to extinction up to four times longer in the adaptive than in the random dispersal mode (Figure 4.2C, D). In the random dispersal mode, species went extinct during simulation time for three out of five dispersal distances under 1°C of warming over 100 years, while extinction was not observed during simulation time under

matching habitat choice (Figure 4.2C). For faster climate change, matching habitat choice always extended time to extinction compared to random dispersal (Figure 4.2D).

Matching habitat choice decreased spatial range loss owing to fewer local extinctions both at the edges of the spatial range and within the spatial range compared to random dispersal. The spatial range was less contracted in the matching habitat choice mode (Figure 4.3A, B), because the colonizing front was moving faster (Figure 4.4 and Figure S4.5). This faster colonizing front, closer to the speed of climate change, was explained by individuals moving more in the direction of their shifting climatic niche when dispersal was adaptive (Figure 4.4 and Figure S4.5). It promoted species' range shift and reduced population extinction at the edges of the distribution. However for the lowest dispersal distance, the speed of the colonizing front was slower than the speed of the climate, meaning that the range was not shifting as fast as the climatic niche in the case of matching habitat choice, leading to important range size reduction. For higher dispersal distances, the speed of the colonizing front was as fast as or even faster than the speed of climate evolution in the case of matching habitat choice (Figure 4.4C,E). This was never the case in the random dispersal mode. The speed of the colonizing front could be faster than the speed of climate in case of matching habitat choice because of mutations. Mutations allowed new phenotypes to appear and these phenotypes, when dispersal distance was sufficient, could colonize new habitats at the cold margin of the range. Matching habitat choice promoted such colonization and we thus observed a faster colonizing front than the speed of the climate only in the case of matching habitat choice mode. When mutation rate was low, the speed of the colonizing front never overtook the speed of the climate (Figure S4.6).

For all parameter values, matching habitat choice also reduced local population extinctions within the spatial range (Figure 4.3D,E) compared to random dispersal mode. Under random dispersal mode, extinctions within the range often occurred right behind the colonizing front (Figure S4.7B). Local maladaptation was indeed high at this location (Figure S4.7C) because of the non-adaptive gene flow preventing any change in the mean populations' phenotype in response to climate change (Figure S4.7D). Under matching

habitat choice, adaptive gene flow prevented strong maladaptation behind the colonizing front, reducing fragmentation of the range (Figure S4.7).

The influence of matching habitat choice on species' response to climate change could be explained by adaptive emigration, adaptive immigration or the combination of both. When we modeled adaptive immigration with no adaptive emigration, most results were similar to the scenario where both emigration and immigration were adaptive. Indeed, the spatial range was better maintained (Figure S4.8A,B), less contracted (Figure S4.9A,B) and – to a lesser extent – less fragmented (Figure S4.9C,D) and the extinction time was longer (Figure S4.8C,D) than under random dispersal for most parameter values. On the contrary, the results with adaptive emigration and no adaptive immigration were similar to those obtained under random dispersal (Figures S4.8, S4.9).

Dispersal distance had a strong influence on observed patterns. The higher the dispersal distance was, the higher the thermal survival probabilities of residents, of immigrants and of emigrants were, particularly in the matching habitat choice mode (Figure 4.1B, Figure S4.3B, S4.4B). While dispersal was always adaptive under matching habitat choice (Figure 4.1A, Figure S4.3A, S4.4A), dispersal distance had to be sufficiently high to maintain a high survival probability through time for all individuals (Figure 1B, Figure S4.3B, S4.4B). As dispersal distance positively influenced thermal survival probability, it also positively influenced range loss limitation, time of persistence, limitation of range contraction and range fragmentation (except under random dispersal for a warming of 2°C/100 years; see below) and colonization success in the two dispersal modes (Figures 4.2, 4.3, 4.4). However, its effect was much larger in the matching habitat choice mode than in the random dispersal mode. For example, an increase of 1 unit in dispersal distance induced a 12% reduction in range loss under random dispersal whereas the same increase allowed a shift from a range loss of 45% to a range expansion of 20% under matching habitat choice (Figure 4.2A; dispersal distance of 2 and 3 units). Dispersal distance also promote species range shift under climate change by increasing the speed of the colonizing front in both random dispersal and matching habitat choice (Figure 4.4). However, despite the positive influence of dispersal distance, matching habitat choice promoted species' responses

to climate change compared to random dispersal even for low dispersal distances (i.e. 2 space units).

The only situation where dispersal distance did not positively influence species' response to climate change was for range contraction under random dispersal and a warming of 2°C/100 years (Figure 4.3D). In this case, fragmentation was higher for intermediate dispersal distance than for low and high dispersal distances. At low dispersal distance, the range was nearly extinct after 100 years of warming (range loss equal to 1 in case of random dispersal with a dispersal distance of 2 space unit; Figure 4.2B), preventing fragmentation from being high (if the range is small, extinction within the range should be rare). When dispersal distance increased, the part of the range that remained after 100 years of warming also increased (Figure 4.2B) allowing fragmentation to rise (Figure 4.3D).

In addition to dispersal distance, we explored the influence of the major demographic parameters of the model that are survival probability, fecundity, carrying capacity and emigration probability, on species' responses to climate change. We found that our conclusions held for the different parameter values we tested for. In all cases, matching habitat choice reduced range loss during climate change compared to random dispersal (Figure 4.5). For the majority of parameter values, matching habitat choice also extended extinction time, reduced range contraction and range fragmentation (Figure S4.12, S4.13, S4.14). The higher the survival probability, fecundity, carrying capacity or emigration probability was, the lower the range loss during climate change was for both species performing matching habitat choice and random dispersal. Range loss during climate change however depended much more on survival probability and fecundity than on carrying capacity which had a very low impact (Figure 4.5). Interestingly, emigration probability had a greater impact on species performing matching habitat choice than on those dispersing randomly. For example, a 0.4 increase in juveniles emigration probability reduced range loss of 0.25 during climate change with random dispersal whereas a 0.1 increase in juveniles emigration probability reduced range loss of 0.6 with matching habitat choice (Figure 4.5, warming = 1°C/100 years).

We also tested for the influence of other factors involved in dispersal decisions such as conspecific density. We found that matching habitat choice depending on temperature and local density improved the persistence of populations (i.e. lower extinction rate (Figure S4.12A,B) and extended time to extinction (Figure S4.12C,D)) compared to random dispersal, by reducing range contraction (Figure S4.13A,B) and range fragmentation (Figure S4.13C,D). Differences between results with and without the dependency of matching habitat choice on local density were well below the range of differences observed between matching habitat choice and random dispersal modes (Figure 4.2 and 4.3 versus Figure S4.12 and S4.13).

Finally, our conclusions also held for the different levels of spatio-temporal environmental stochasticity we tested for, while stochasticity led to less adaptive dispersal decisions. For all parameters values, spatial range loss for matching habitat choice during climate change was lower than, or at least equal to random dispersal (Figure 4.6). For the majority of parameter values, matching habitat choice also extended extinction time, reduced range contraction and range fragmentation (Figure S4.15, S4.16, S4.17). In both dispersal modes, spatial range loss was positively correlated to environmental stochasticity. However, in most cases, environmental stochasticity had a stronger impact on range loss for the matching habitat choice mode than for the random dispersal mode (Figure 4.6A). Indeed, for the different dispersal distances tested, range loss under climate change in case of random dispersal was not impacted by low to moderate environmental stochasticity while range loss was impacted under matching habitat choice, confirming the negative influence of environmental stochasticity on the optimality of matching habitat choice. Under very high environmental stochasticity, range loss strongly increased for both dispersal modes. For this high environmental stochasticity, species went extinct in both random dispersal and matching habitat choice for low dispersal distance and a warming of 2°C/100 years (Figure 4.6B) such that the benefit of matching habitat choice on species range loss compared to random dispersal was lost.

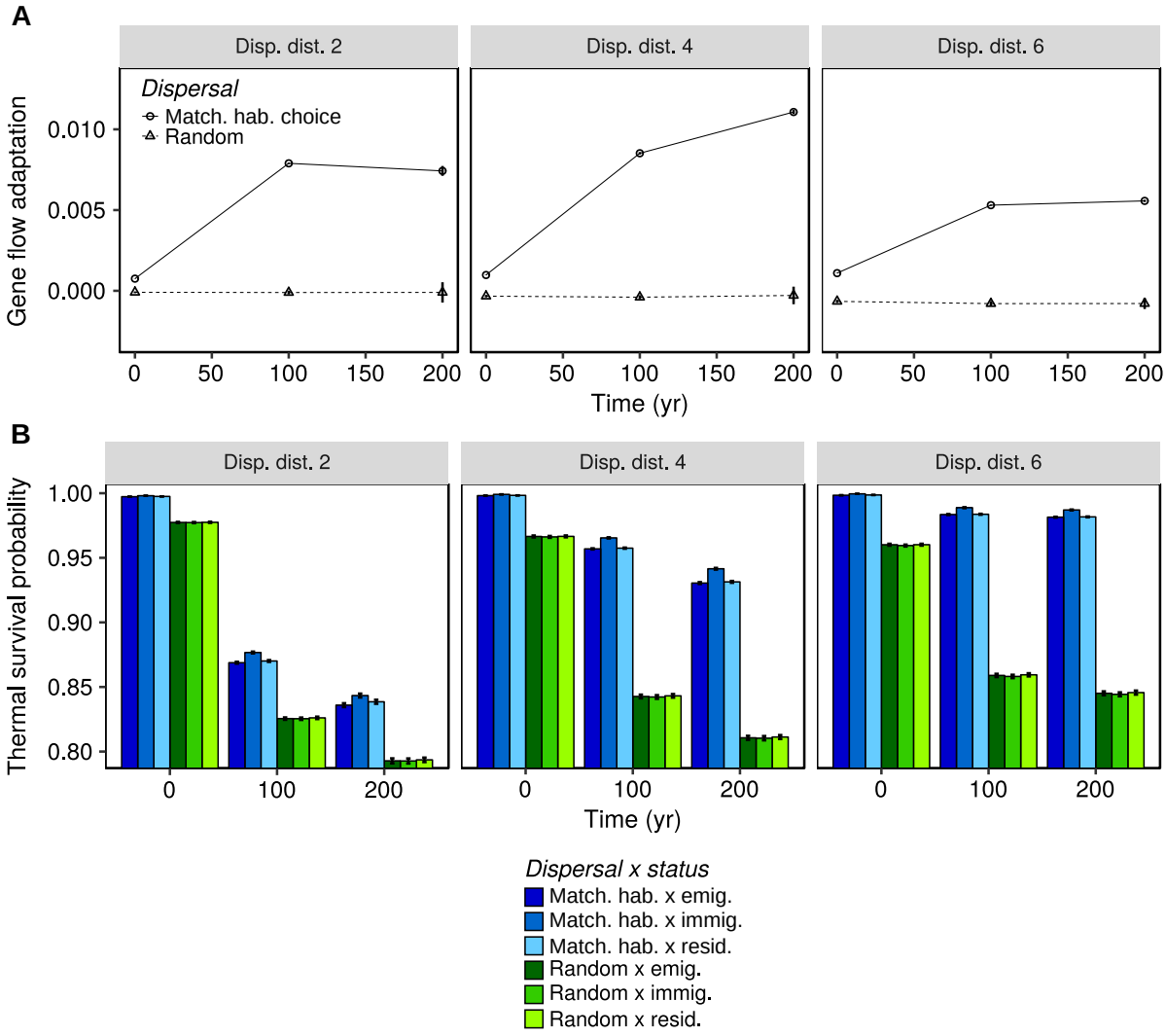

Figure 4.1 – Adaptiveness of gene flows and thermal survival probability. Adaptiveness of the gene flow (A) and the thermal survival probability of emigrants, immigrants and residents (B) through time for different dispersal distances in case of matching habitat choice (circles and solid lines (A) and blue bars (B)) or random dispersal (triangles and dashed lines (A), and green bars (B)). Results were obtained under a climate change scenario of 1°C of warming over 100 years. A) Thermal adaptiveness of total gene flow through time for different dispersal distances for the matching habitat choice (black) and random dispersal (white) scenarios (see methods for details). B) Thermal survival probability of emigrants (dark blue for matching habitat choice, dark green for random dispersal), immigrants (medium blue for matching habitat choice, medium green for random dispersal) and residents (light blue for matching habitat choice, light green for random dispersal) through time for different dispersal distances in case of matching habitat choice (blue bars) and random dispersal (green bars). Means (±SD) over 50 simulations are shown.

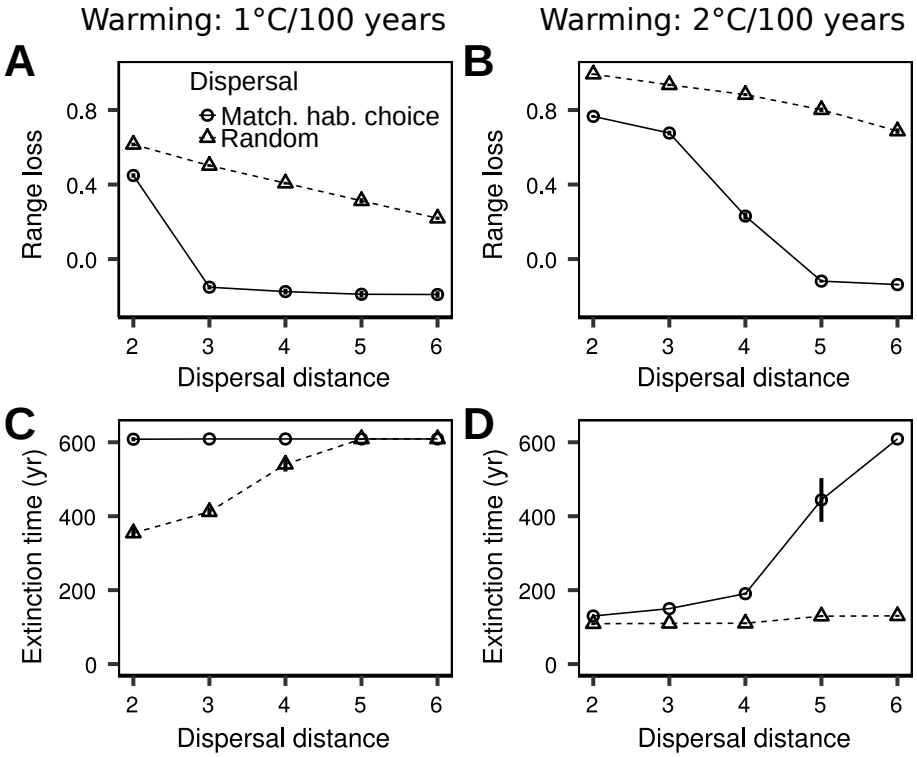

Figure 4.2 – Consequences of adaptive gene flow on species responses to climate change. Proportion of spatial range loss (A,B) and extinction time (C,D) depending on dispersal distance in case of matching habitat choice (black bars) or random dispersal (white bars) and for two climate change scenarios (scenario A,C: 1°C/100 years, scenario B,D: 2°C/100 years). Spatial range loss was measured after 200 years of warming for scenario A and after 100 years of warming for scenario B. When the species persisted until the end of simulations (600 years), the extinction time was indicated as 600 years. Means (± SD) over 50 simulations are shown.

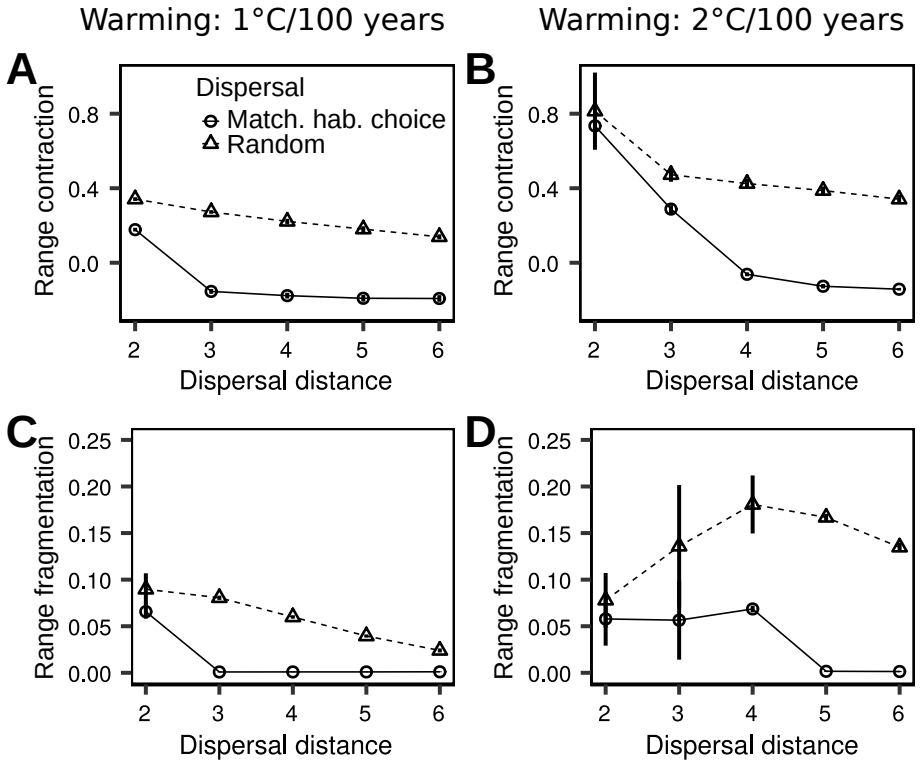

Figure 4.3 – Spatial range contraction and fragmentation. Proportion of spatial range contraction (A,B) and spatial range fragmentation (C,D) depending on dispersal distance in case of matching habitat choice (black bars) or random dispersal (white bars) and for two climate change scenarios (scenario A,C: 1°C/100 years, scenario B,D: 2°C/100 years). Spatial range contraction was measured after 200 years of warming for scenario A and after 100 years of warming for scenario B. Spatial range fragmentation was measured between 0 and 200 years of warming for scenario C and between 0 and 100 years of warming for scenario D. Means (± SD) over 50 simulations are shown.

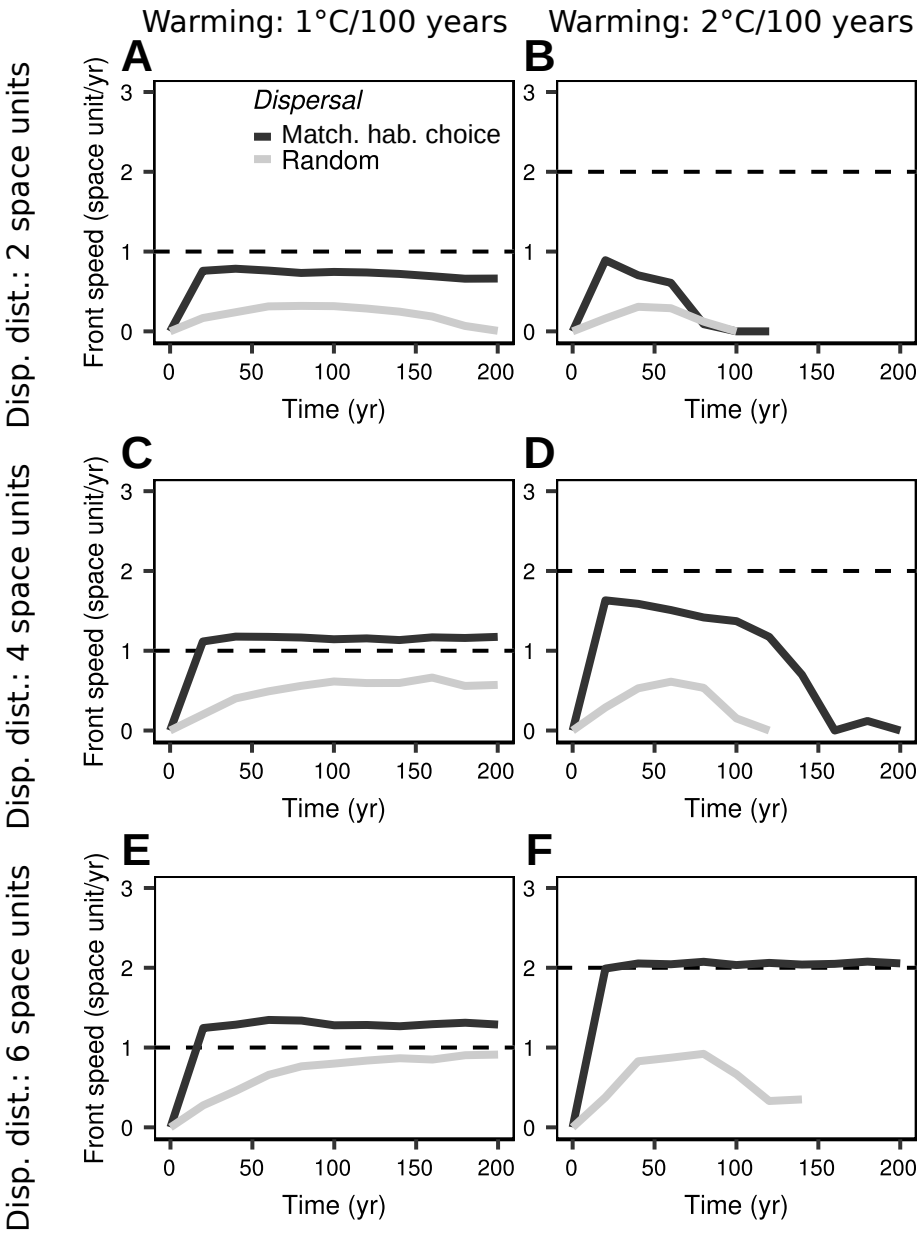

Figure 4.4 – Colonization dynamics. Mean speed dynamics of colonizing front though time in case of matching habitat choice (black solid line) or random dispersal (light gray solid line) and for two climate change scenarios (scenario A,C,E: 1°C/100 years, scenario B,D,F: 2°C/100 years). To keep up with the pace of climate change, the front speed should be as high as the dashed line. Three different dispersal distances were tested: 2 space units (scenarios A,B), 3 space units (scenarios C,D) and 4 space units (scenarios E,F). Mean curves over 50 simulations are shown.

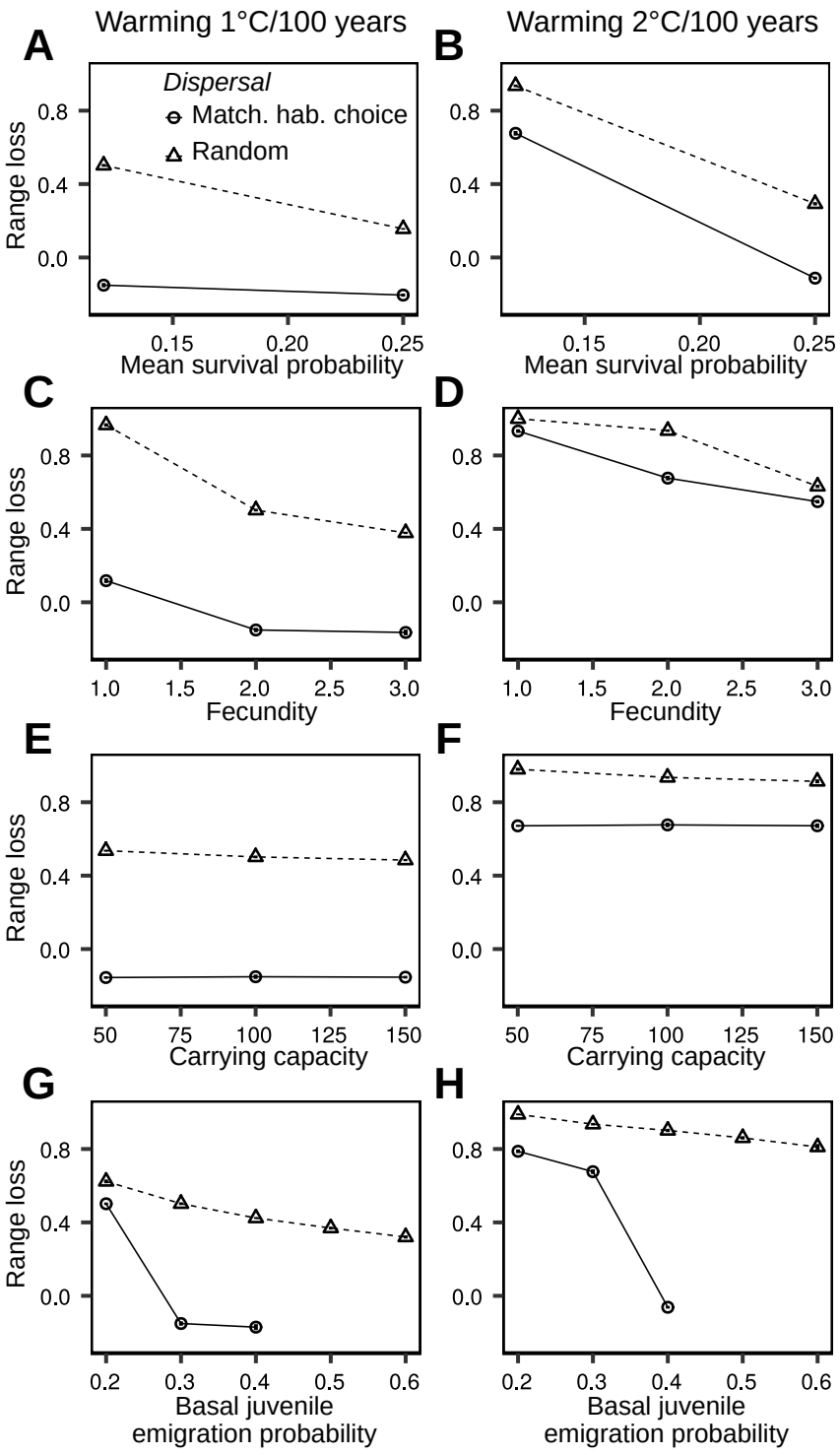

Figure 4.5 – Influence of demographic parameters on spatial range loss during climate change. Proportion of spatial range loss depending on survival probability (A,B), fecundity (C,D), carrying capacity (E,F) and emigration probability (G,H) in case of matching habitat choice (open circle, solid line) or random dispersal (open triangle, dashed line) and for two climate change scenarios (scenario A,C,E,G: 1°C/100 years, scenario B,D,F,H: 2°C/100 years). Spatial range loss was measured after 200 years of warming for scenario A,C,E,G and after 100 years of warming for scenario B,D,F,H. See section "Legend details" in supplementary materials for additional information. Means (± SD) over 50 (parameter values of main simulations (Table 4.1)) or 20 (parameter values of extra simulations (Table 4.1)) simulations are shown.

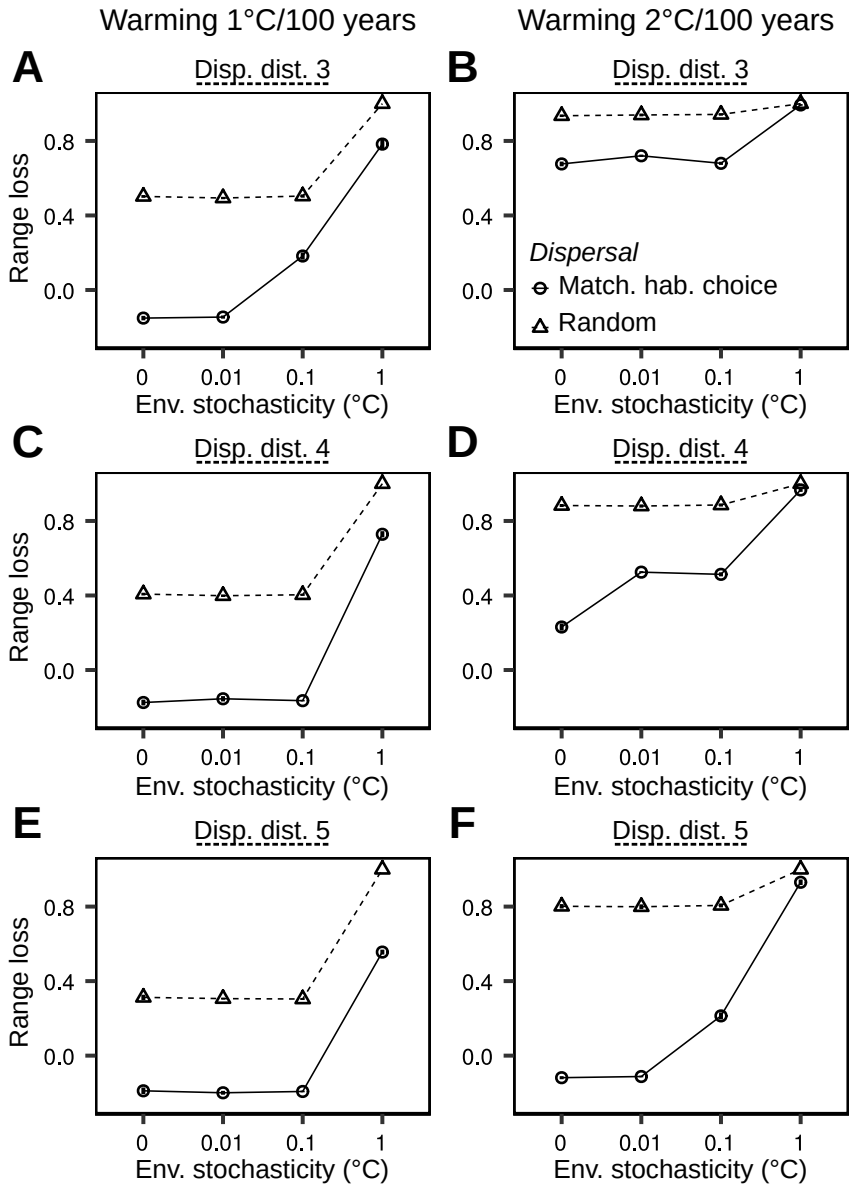

Figure 4.6 – Influence of environmental stochasticity on spatial range loss during climate change. Proportion of spatial range loss depending on environmental stochasticity in case of matching habitat choice (circles and solid lines) or random dispersal (triangles and dashed lines) for different dispersal distances (A,B: 3 space units; C,D: 4 space units; E,F: 5 space units) and for two climate change scenarios (scenario A,C,E: 1°C/100 years, scenario B,D,F: 2°C/100 years). The level of environmental stochasticity determined how much the temperature of habitats on a given latitude could vary around the current mean temperature of this latitude (see methods section for details). Spatial range loss was measured after 200 years of warming for scenario A,C,E and after 100 years of warming for scenario B,D,F. Means (± SD) over 50 (parameter values of main simulations (Table 4.1)) or 20 (parameter values of extra simulations (Table 4.1)) simulations are shown.

5 Discussion

In this study, we demonstrated that matching habitat choice induces an adaptive gene flow enhancing individuals' mean survival probability, reducing population extinction risk and improving species persistence under climate change compared to random dispersal. We investigated the influence of matching habitat choice on population dynamics and adaptation, revealing the specific mechanisms by which this local-scale dispersal strategy increases population persistence under climate change at a larger scale. Matching habitat choice (i) promotes colonization and therefore species' range expansion and (ii) reduces population extinction within the range and therefore range fragmentation. Predictions for the probability of extinction and for the time to extinction under random dispersal and matching habitat choice greatly differed in magnitude. We even found qualitatively different predictions in some cases, where the model predicted range contraction under random dispersal while it predicted range expansion under matching habitat choice, especially for large dispersal distances (Figure 4.2, 4.3). The predicted differences for the time to extinction can be so large that the species was predicted to go extinct in 200 years in the random dispersal mode while no extinction was recorded for 600 years of continuing climate change in the matching habitat choice mode. Therefore, for species performing matching habitat choice efficiently, this dispersal mode has to be considered when predicting populations' range shift and extinction risk.

In our model, the benefits of matching habitat choice on species' responses to climate change depend much more on adaptive immigration than emigration decisions (Figure S4.8, S4.9). Emigration decisions depend on individuals gathering information on local thermal conditions and assessing their phenotypic match to these conditions while immigration decisions entail a comparison of thermal conditions throughout the environment. Individuals would therefore have to visit numerous candidate habitats to choose the most suited one (Delgado *et al.*, 2014). Species with low prospecting and dispersal abilities should thus be more at risk facing climate change as they might not be able to visit enough patches to choose habitats adaptively (Edelaar *et al.*, 2008). However,

accumulating studies evidenced fine-tuned processes underlying informed dispersal and many species may gather information on surrounding habitats before emigration (Cote & Clobert, 2007a; Jacob *et al.*, 2015b). These additional processes may reinforce the effects of adaptive immigration decisions by allowing species to orient their movements towards habitats with suitable thermal conditions.

The benefits of performing matching habitat choice compared to random dispersal may therefore depend on species ability to disperse and to gather accurate information on thermal conditions. Our results indeed show that dispersal distance and emigration probability positively influenced the benefit of adaptive gene flow - resulting from matching habitat choice - on population persistence, range fragmentation and range shift as a minimal dispersal distance is required to maintain a high survival probability through time. The minimal dispersal distance corresponded here to a distance from two to three times the distance at which the climatic niche was moving from low to high latitudes (e.g. minimal dispersal distance from 2 space units for a warming of 1°C/100 years). In the conditions of our model, 2 space units corresponded to 0.02°C variations along the gradient. In the real world, a typical annual temperature decrease with latitude is -0.75°C per degree latitude (en Van de Water *et al.*, 1994). Given that one degree latitude corresponds approximately to 110 km around 45° latitude, dispersal distances of 2 space units in our model correspond to distances of 2.93 km for temperate areas. Such distance might be achievable by many species as the mean maximum dispersal distance for species dispersing actively was found to be 9.12 km (Jenkins *et al.*, 2007). We found that above this minimal dispersal distance, species could track climate change without suffering range size reduction. Overall, species with lower dispersal abilities should therefore be more at risk from climate change because they might not be able to track suitable climatic conditions and to choose habitats adaptively (Pearson, 2006; Schloss *et al.*, 2012).

We think our model could be applied to a large variety of species with good movement skills. However, as outlined above, our model is restricted to species able to perceive variation in thermal conditions and perform matching habitat choices accordingly. Matching habitat choice might therefore be easier to perform on an altitudinal than on a latitudi-

nal axis because of the steeper thermal gradients. In mountain areas, temperature can strongly vary at local spatial scales, allowing species with low dispersal ability and/or low thermal sensitivity to detect and choose habitats with suitable microclimates. However, in lowland areas, species may also be able to perform matching habitat choice as implemented in our model. Climate change may induce important variations during a restricted period of the year (e.g. summer) while changes in mean annual temperature would appear small as in our model. These punctual variations might be enough to influence species dispersal, especially for ectotherms in which small variations near the upper physiological thermal limits induce important fitness changes (Huey *et al.*, 2012). The pertinence of matching habitat choice should nonetheless be ascertained on a case-by-case basis.

Our conclusions may further depend on the optimality of dispersal decisions. Suboptimal emigration and immigration decisions can result from low prospecting skills and from variability in climatic conditions and environmental conditions induced by habitat fragmentation or environmental stochasticity. Indeed, in our model, environmental stochasticity led to suboptimal immigration decisions due to temporal low predictability of the climate and to increased range loss in the matching habitat choice mode. Induced suboptimal decisions however still increased species persistence under climate change in comparison to random dispersal. This is in accordance with the observations of Edelaar & Bolnick (2012) on population adaptation and differentiation under stable climate for random, suboptimal and optimal immigration decisions. Similarly to environmental stochasticity, landscape fragmentation magnifies dispersal costs and should therefore hamper the exploration of surrounding habitats reducing the optimality of dispersal decisions (Jacob *et al.*, 2015a; Cote *et al.*, 2017). Landscape fragmentation might therefore decrease the observed benefits of matching habitat choice and might underpin the expected synergetic effects of climate change and fragmentation on population persistence and spatial range shift dynamics (Brook *et al.*, 2008). This hypothesis remains to be tested. Finally, habitat choice may also become suboptimal in the presence of other major dispersal drivers. For example, intraspecific competition may influence individuals' fitness differently than local thermal conditions (Paterson & Blouin-Demers, 2018). Matching habitat choice may

therefore depend on adaptation to both local climates and local density. In our model, the responses to climate warming were similar when matching habitat choice depended on both thermal adaptation and local density and when matching habitat choice depended on thermal adaptation only (Figure S4.12, S4.13). On top of those discussed above, we expect our conclusions to hold qualitatively for other sources of variation in the optimality of habitat choice.

Some other assumptions of our model may be critical to our results. Among these assumptions, selection occurred on survival only. Survival, but not reproductive success, depended on local temperature and density. It implies that non-adapted individuals could reproduce and transmit their genes to the next generation before dying. It should therefore slow down the adaptive process and increase the impact of non-adapted gene flow on population adaptation under random dispersal. If selection was occurring on both reproduction and survival, selection would be stronger and adaptation faster, reducing the transmission of maladapted genes to the next generation and thus the impact of maladapted individuals. As a consequence, it should limit the influence of maladaptive gene flow under random dispersal that is involved in range limitation under stable climate (Kirkpatrick & Barton, 1997; Lenormand, 2002; Bridle & Vines, 2007) and may reduce the observed differences in population extinction and species' range shift between random dispersal and matching habitat choice. However, our conclusions should qualitatively hold as matching habitat choice promotes dispersal and gene flow in the direction of the moving climatic niche compared to random dispersal. Colonization of new habitats should therefore remain higher under matching habitat choice than under random dispersal.

Matching habitat choice positively influenced species' responses to climate change by limiting the mismatches between individuals' phenotypes and local environments (Figure 1A). Phenotypic plasticity may also limit such mismatches. Phenotypic plasticity has been demonstrated to influence species' responses to climate change by limiting range size reduction (Valladares *et al.*, 2014). Recent models allowing evolution of both matching habitat choice and phenotypic plasticity demonstrated that under temporally stable climate (i.e. no change in the mean temperature in the landscape but environmental

stochasticity integrated), phenotypic plasticity evolved more frequently than matching habitat choice (Scheiner, 2016; Edelaar *et al.*, 2017). However under climate change, phenotypic plasticity might delay evolutionary response in the long term, whereas matching habitat choice promotes it by inducing an adaptive gene flow (Valladares *et al.*, 2014). Under such conditions, the benefit of phenotypic plasticity could be lower than those of matching habitat choice, promoting the evolution of the latter. On the other hand, phenotypic plasticity could limit the mismatch between phenotypes and climate until the limits of plasticity are reached. If plasticity evolved, it could allow further coping with environmental change without any evolutionary change of the traits under selection. Depending on the cost of plasticity and matching habitat choice, both mechanisms could thus evolve to facilitate species' responses to climate change. Future models could tackle this question by allowing the evolution of both phenotypic plasticity and matching habitat choice under a continuous period of climate change.

The influence of informed dispersal on local adaptation and population differentiation has been theoretically well-studied (Holt, 1987; Armsworth & Roughgarden, 2005b,a, 2008; Ravigné *et al.*, 2009; Bolnick & Otto, 2013; Holt & Barfield, 2015)). Others have investigated its evolution under various conditions (Travis *et al.*, 1999, 2009; Hovestadt *et al.*, 2010; Scheiner, 2016; Edelaar *et al.*, 2017) and its feedback effect on dispersal propensity, range limits and range expansion (Enfjäll & Leimar, 2009; Kubisch *et al.*, 2010, 2011; Bocedi *et al.*, 2014; Poethke *et al.*, 2016). Here we investigated the effect of a particular type of informed dispersal, matching habitat choice, on species' responses to climate change. Using a simple model with robust predictions, we showed that neglecting these mechanisms may lead to inaccurate estimates of species extinction risk and spatial range shift. Similarly, matching habitat choice should greatly affect predictions of population dynamics, evolutionary adaptation, species interactions, and changes in community composition in response to climate warming. While our model focused on the match between thermal optimum and external temperature, conclusions should be similar for any other phenotypic trait interacting with environmental variables affected by contemporary global change (e.g. hygrometry and UV intensity). We therefore recommend future

research to pay more attention to matching habitat choice when studying populations' dynamics and spatial range shift to improve model predictions and management policies.

6 Supplementary materials

Legend details

Figure 4.5: In A,B) only juvenile survival probability was represented but it was associated with adult survival probability (0.5 for juvenile survival probability of 0.12 and 0.6 for juvenile survival probability of 0.25). In G,H the x axis represented the basal juvenile emigration probability. It was associated with an adult emigration probability (0.05 for the basal juvenile emigration probability of 0.2, 0.15 for the basal juvenile emigration probability of 0.4, 0.25 for the basal juvenile emigration probability of 0.4, 0.35 for the basal juvenile emigration probability of 0.5 and 0.45 for the basal juvenile emigration probability of 0.6). In case of random dispersal emigration probabilities for juveniles and adults was fixed whereas emigration probabilities could vary in case of matching habitat choice (from 0.2 to 0.4 and 0.05 to 0.25 for juveniles and adults respectively for the basal juvenile emigration probability of 0.2; from 0.3 to 0.5 and 0.15 to 0.35 for juveniles and adults respectively for the basal juvenile emigration probability of 0.3; from 0.4 to 0.6 for juveniles and adults respectively for the basal juvenile emigration probability of 0.4).

Figure S4.12: In A,B) only juvenile survival probability was represented but it was associated with adult survival probability (0.5 for juvenile survival probability of 0.12 and 0.6 for juvenile survival probability of 0.25). In G,H the x axis represented the basal juvenile emigration probability. It was associated with an adult emigration probability (0.05 for the basal juvenile emigration probability of 0.2, 0.15 for the basal juvenile emigration probability of 0.4, 0.25 for the basal juvenile emigration probability of 0.4, 0.35 for the basal juvenile emigration probability of 0.5 and 0.45 for the basal juvenile emigration probability of 0.6). In case of random dispersal emigration probabilities for juveniles and adults was fixed whereas emigration probabilities could vary in case of matching habitat choice (from 0.2 to 0.4 and 0.05 to 0.25 for juveniles and adults respectively for the basal

juvenile emigration probability of 0.2; from 0.3 to 0.5 and 0.15 to 0.35 for juveniles and adults respectively for the basal juvenile emigration probability of 0.3; from 0.4 to 0.6 for juveniles and adults respectively for the basal juvenile emigration probability of 0.4). Overall the results were the same as in Figure 4.5: Extinction time was always higher or the same in case of matching habitat choice than in case of random dispersal. Survival probability, fecundity and emigration probability had a positive influence on extinction time.

Figure S4.13: In A,B) only juvenile survival probability was represented but it was associated with adult survival probability (0.5 for juvenile survival probability of 0.12 and 0.6 for juvenile survival probability of 0.25). In G,H the x axis represented the basal juvenile emigration probability. It was associated with an adult emigration probability (0.05 for the basal juvenile emigration probability of 0.2, 0.15 for the basal juvenile emigration probability of 0.4, 0.25 for the basal juvenile emigration probability of 0.4, 0.35 for the basal juvenile emigration probability of 0.5 and 0.45 for the basal juvenile emigration probability of 0.6). In case of random dispersal emigration probabilities for juveniles and adults was fixed whereas emigration probabilities could vary in case of matching habitat choice (from 0.2 to 0.4 and 0.05 to 0.25 for juveniles and adults respectively for the basal juvenile emigration probability of 0.2; from 0.3 to 0.5 and 0.15 to 0.35 for juveniles and adults respectively for the basal juvenile emigration probability of 0.3; from 0.4 to 0.6 for juveniles and adults respectively for the basal juvenile emigration probability of 0.4). Overall the results were the same as in Figure 4.5 and Figure S4.12: Range contraction was always lower in case of matching habitat choice than in case of random dispersal. Survival probability, fecundity and emigration probability had a negative influence on spatial range contraction.

Figure S4.14: In A,B) only juvenile survival probability was represented but it was associated with adult survival probability (0.5 for juvenile survival probability of 0.12 and 0.6 for juvenile survival probability of 0.25). In G,H the x axis represented the basal juvenile emigration probability. It was associated with an adult emigration probability (0.05 for the basal juvenile emigration probability of 0.2, 0.15 for the basal juvenile emigration

probability of 0.4, 0.25 for the basal juvenile emigration probability of 0.4, 0.35 for the basal juvenile emigration probability of 0.5 and 0.45 for the basal juvenile emigration probability of 0.6). In case of random dispersal emigration probabilities for juveniles and adults was fixed whereas emigration probabilities could vary in case of matching habitat choice (from 0.2 to 0.4 and 0.05 to 0.25 for juveniles and adults respectively for the basal juvenile emigration probability of 0.2; from 0.3 to 0.5 and 0.15 to 0.35 for juveniles and adults respectively for the basal juvenile emigration probability of 0.3; from 0.4 to 0.6 for juveniles and adults respectively for the basal juvenile emigration probability of 0.4). Overall the results were the same as in Figure 4.5, Figure S4.12 and Figure S4.13: For most parameters values range fragmentation was lower in case of matching habitat choice than in case of random dispersal. Range fragmentation was similar between random dispersal and matching habitat choice for the lowest emigration probability and de warming of 1°C/100 years and for le lowest fecundity and a warming of 2°C/100 years.

Figure S4.17: Overall the results were the same as in Figure 4.6, Figure S4.15 and Figure S4.16: For most parameters values range fragmentation was lower in case of matching habitat choice than in case of random dispersal. Range fragmentation was higher for matching habitat choice than for random dispersal for the highest environmental stochasticity and a warming of 2°C/100 years. Environmental stochasticity had a positive influence on range fragmentation for a warming of 1°C/100 years in both random dispersal and matching habitat choice. For a warming of 2°C/100 years, the environmental stochasticity has a positive influence on range fragmentation in case of matching habitat choice and a negative influence on range fragmentation in case of random dispersal. The relation was negative in case of random dispersal because the range was nearly extinction for high environmental stochasticity, preventing fragmentation to occur.

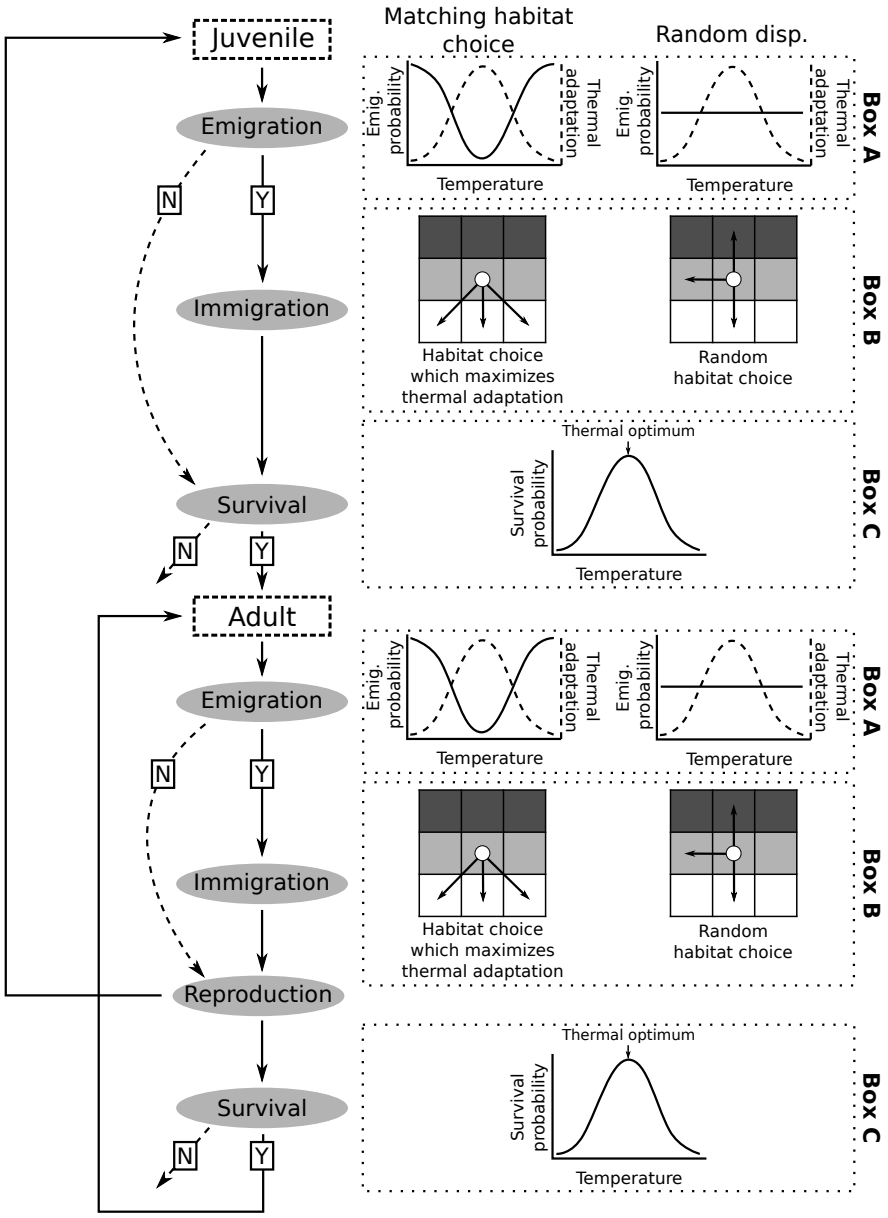

Figure S4.1 – Flow diagram of the model. The left side of this diagram depicts the life cycle of the modeled species. At birth, a Juvenile could disperse (emigration and immigration), then survive to become an adult or die. As an adult, it could disperse again (emigration and immigration), reproduce and survive or die. The adult stage last until the individual died. The right side shows how we modeled the different events of the life cycle (i.e. emigration, immigration, survival) in the matching habitat choice and random dispersal modes. For both modes, survival was a Gaussian function of local temperature (Box C) and so does thermal adaptation (dashed line, Box A). Emigration probability (solid line, Box A) depending on local temperature in the matching habitat choice mode and was constant in the random dispersal mode. After leaving its habitat, an emigrant with a given phenotype (i.e. the color of the circle) settled in a matching habitat choice its phenotype (i.e. same color) for the matching habitat choice mode while it settled in a randomly chosen habitat when dispersal was random (Box B).

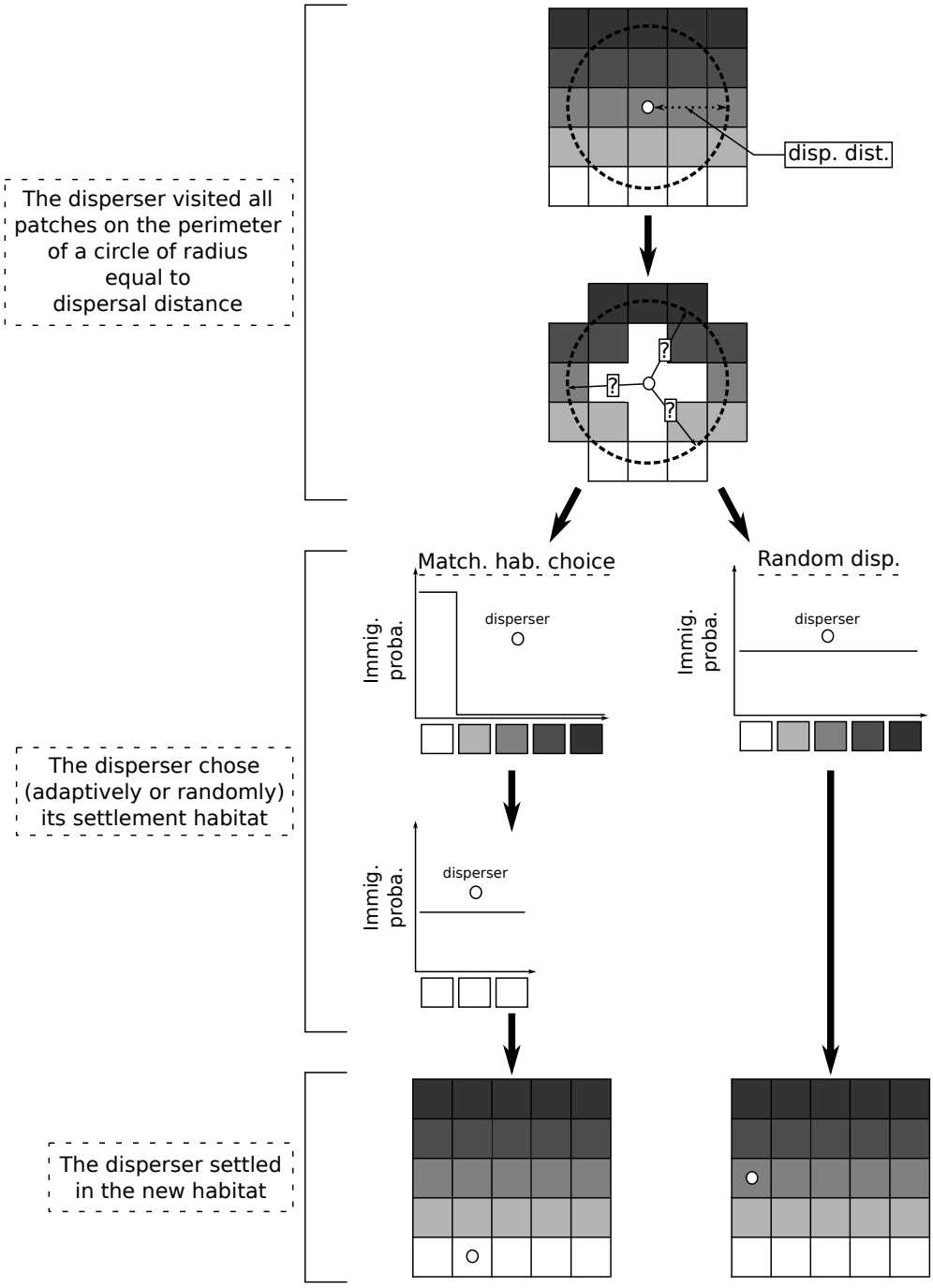

Figure S4.2 – Dispersal rules. Details of the different steps of dispersal for matching habitat choice and random dispersal after emigration decision to settlement. After emigrating, the disperser visited all patches on a the perimeter of a circle of radius equal to dispersal distance. In case of matching habitat choice it chose the settlement habitat that maximized its lifetime reproductive success. When more than one habitat maximized its lifetime reproductive success, the disperser settled in one of these habitat randomly. In case of random dispersal, the dispersers settled in a randomly chosen habitat among all habitats he visited, on the perimeter of a circle of radius equal to dispersal distance.

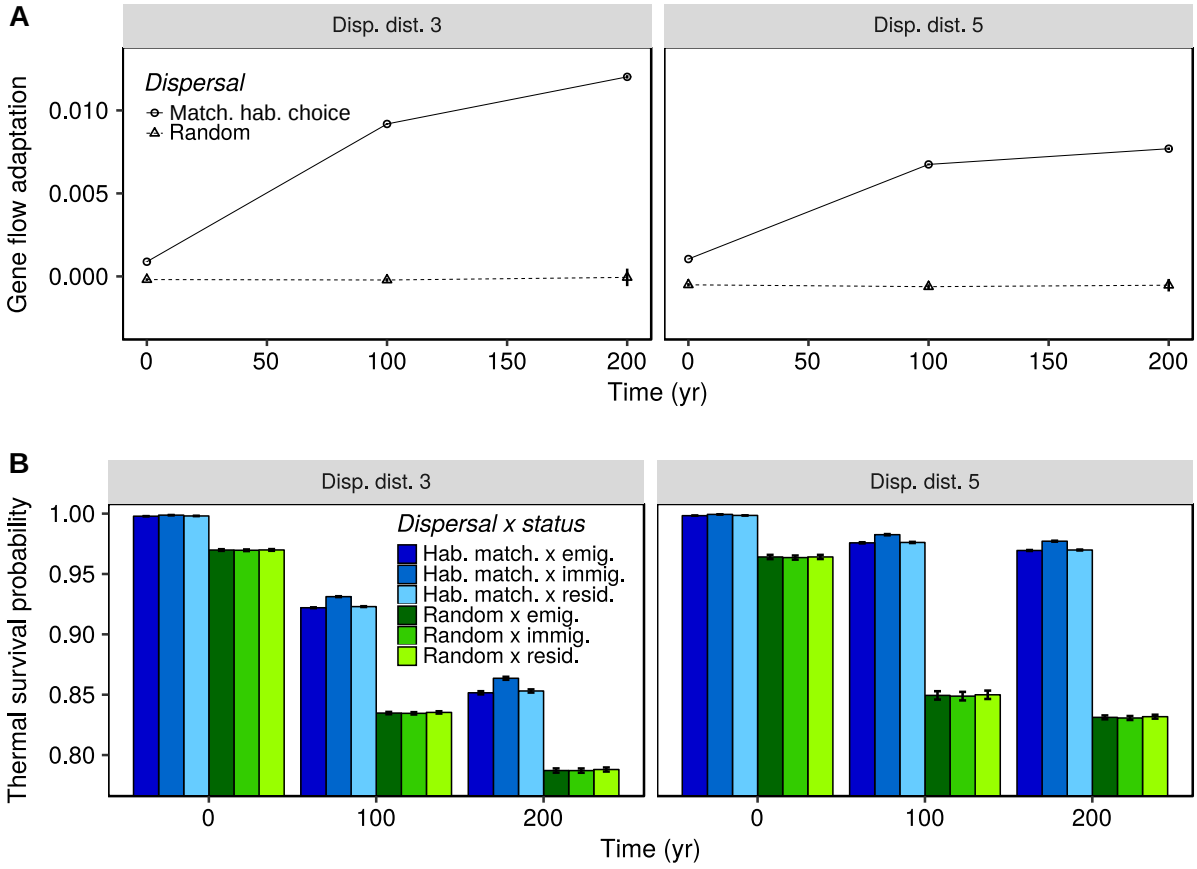

Figure S4.3 – Thermal survival probability and the adaptiveness of gene flows for dispersal distance of 3 and 5 space units and a warming of 1°C/100 years. Same as Figure 4.1 1 but for dispersal distance of 3 and 5 space units: adaptiveness of the gene flow (A) and the thermal survival probability of emigrants, immigrants and residents (B) through time for different dispersal distances in case of matching habitat choice (circles and solid lines (A) and blue bars (B)) or random dispersal (triangles and dashed lines (A), and green bars (B)). Results were obtained under a climate change scenario of 1°C of warming over 100 years. A) Thermal adaptiveness of total gene flow through time for different dispersal distances for the matching habitat choice (black) and random dispersal (white) scenarios (see methods for details). B) Thermal survival probability of emigrants (dark blue for matching habitat choice, dark green for random dispersal), immigrants (medium blue for matching habitat choice, medium green for random dispersal) and residents (light blue for matching habitat choice, light green for random dispersal) through time for different dispersal distances in case of matching habitat choice (blue bars) and random dispersal (green bars). Means (±SD) over 50 simulations are shown.

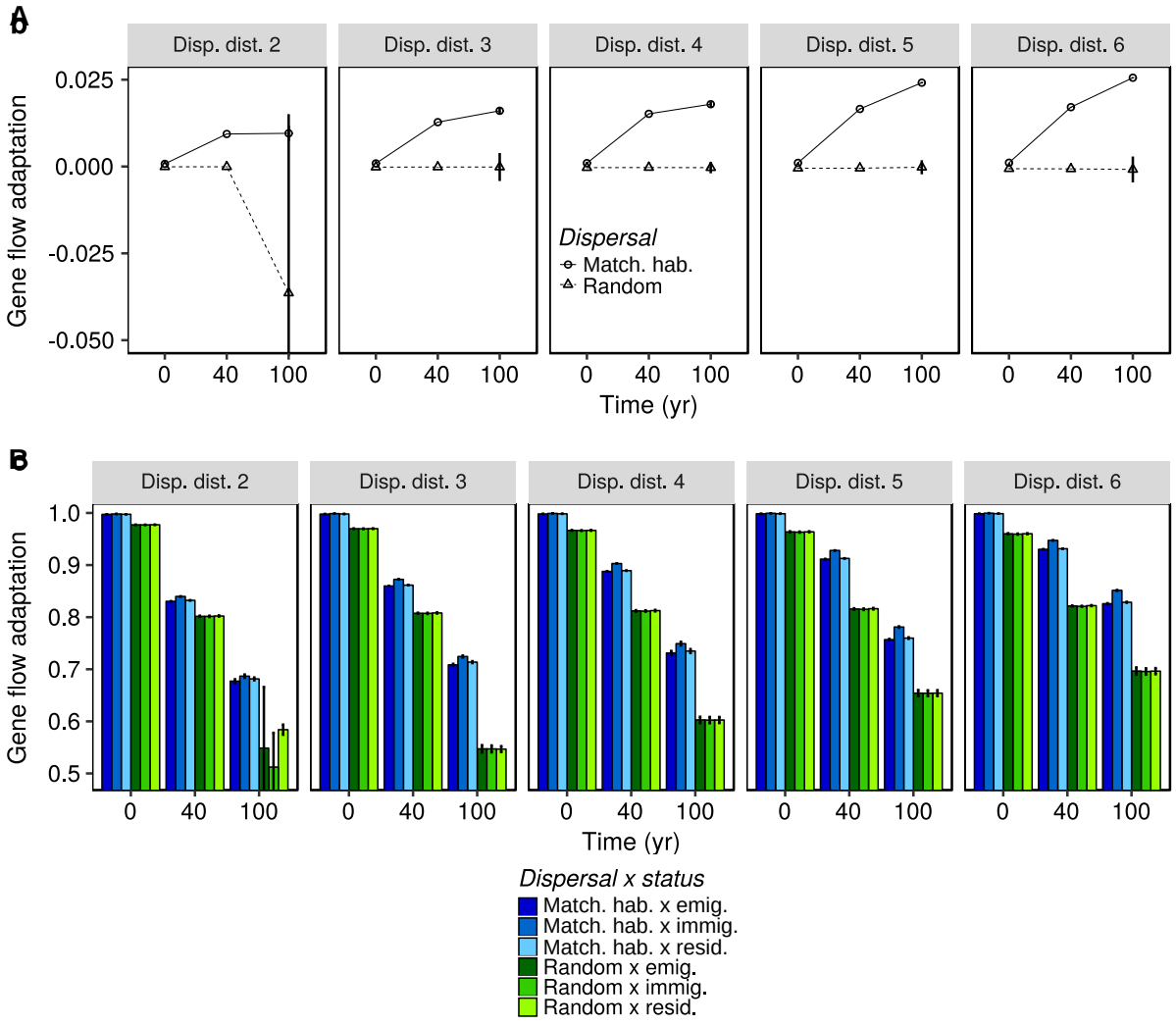

Figure S4.4 – Thermal survival probability and th adaptiveness of gene flows for a warming of 2°C/100 years. Same as Figure 4.1 and Figure S4.3 but for a warming of 2°C/100 years Adaptiveness of the gene flow (A) and the thermal survival probability of emigrants, immigrants and residents (B) through time for different dispersal distances in case of matching habitat choice (circles and solid lines (A) and blue bars (A)) or random dispersal (triangles and dashed lines (A), and green bars (B)). Results were obtained under a climate change scenario of 1°C of warming over 100 years. A) Thermal adaptiveness of total gene flow through time for different dispersal distances for the matching habitat choice (black) and random dispersal (white) scenarios (see methods for details) B) Thermal survival probability of emigrants (dark blue for matching habitat choice, dark green for random dispersal), immigrants (medium blue for matching habitat choice, medium green for random dispersal) and residents (light blue for matching habitat choice, light green for random dispersal) through time for different dispersal distances in case of matching habitat choice (blue bars) and random dispersal (green bars). Means (±SD) over 50 simulations are shown. Overall the observed pattern was the same as in Figure 4.1 and Figure S4.3 but the difference in thermal survival probability between the matching habitat choice mode and the random dispersal mode was higher than for a warming of 1°C/100 years, particularly for large dispersal distance (4, 5, 6 space units). The adaptiveness of gene flow was also higher than for a warming of 1°C/100 years in case of matching habitat choice.

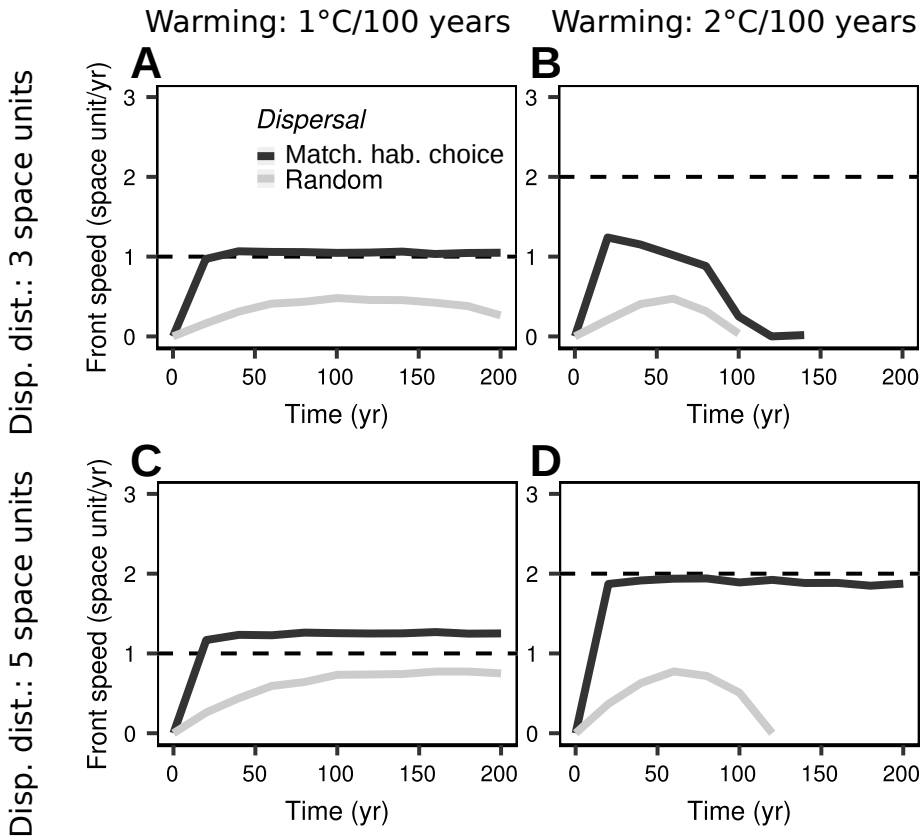

Figure S4.5 – Colonization dynamics for dispersal distance of 5 and 6 space units. Same as Figure 4.4 but for dispersal distance of 3 and 5 space units: mean speed dynamics of colonizing front though time for matching habitat choice (black solid line) or random dispersal (light gray solid line) for two climate change scenarios (scenario A,C: 1°C/100 years, scenario B,D: 2°C/100 years). To keep up with the pace of climate change, the front speed should be at least as high as the dashed line. Two different dispersal distances were tested: 3 space units (scenarios A,B) and 5 space units (scenarios C,D). Mean curves over 50 simulations are shown. In the two climate change scenarios, the colonizing front was moving faster in case of matching habitat choice than in case of random dispersal. For a warming of 1°C/100 years, the colonizing front reached or exceed the speed of the climate in case of habitat. Under random dispersal the colonizing front never kept up with the pace of climate change.

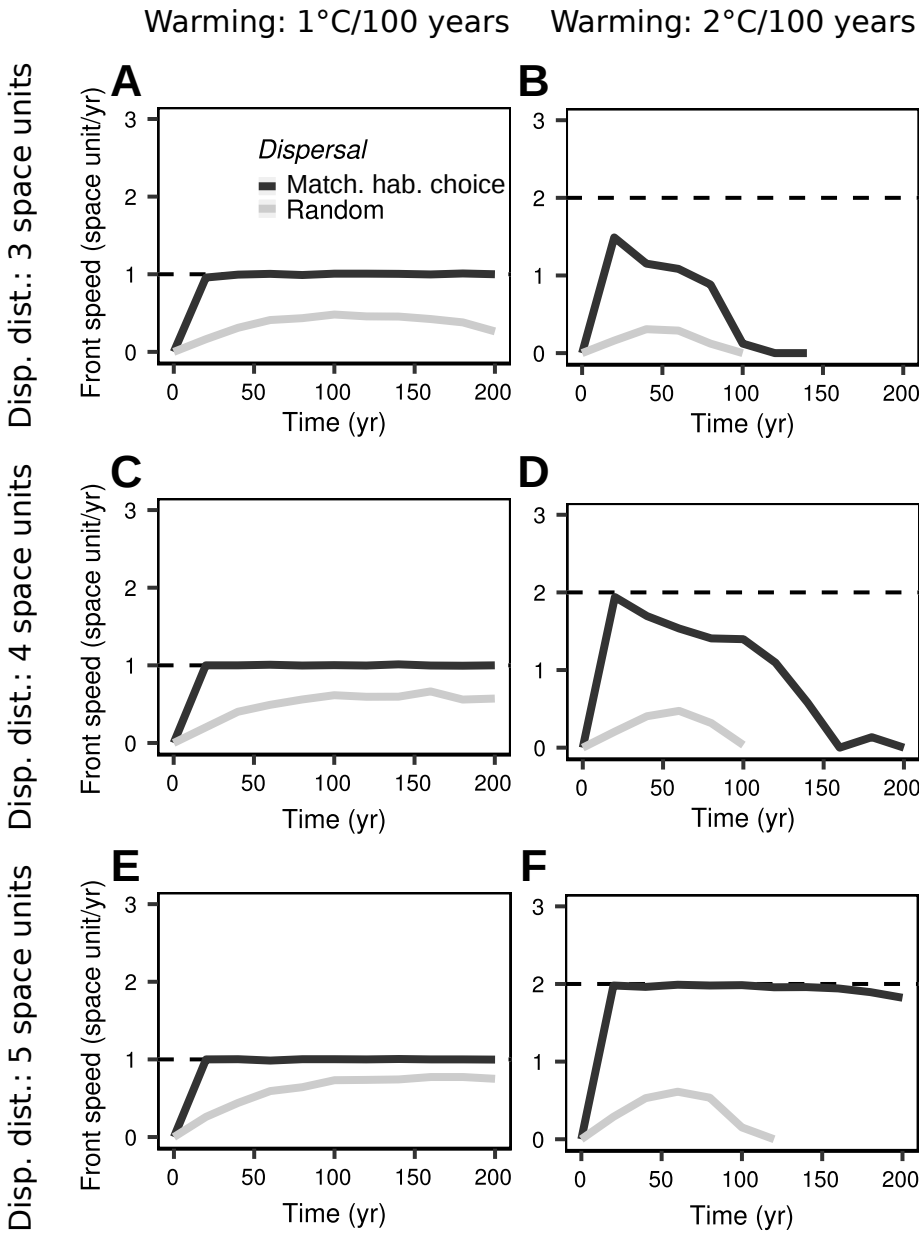

Figure S4.6 – Colonization dynamics for simulations with low mutation rate. Same as in Figure 4.4 and FigureS4.5 but with a mutation rate of 10-7 rather than 10^{-5} and for dispersal distance of 3, 4 and 5 space units only: mean speed dynamics of colonizing front though time for matching habitat choice (black solid line) or random dispersal (light gray solid line) for two climate change scenarios (scenario A,C: 1°C/100 years, scenario B,D: 2°C/100 years). To keep up with the pace of climate change, the front speed should be at least as high as the dashed line. Three different dispersal distances were tested: 3 space units (scenarios A,B), 4 space units (scenarios C,D) and 5 space units (scenarios E,F). Mean curves over 20 simulations are shown. Overall we obtain the same results as in Figure 4.4 and FigureS4.5. The speed of the colonizing front was always higher in case of matching habitat choice than in case of random dispersal. However, the speed of the colonizing front never exceed the speed of the climate in case of matching habitat choice as observed with a higher mutation rate.

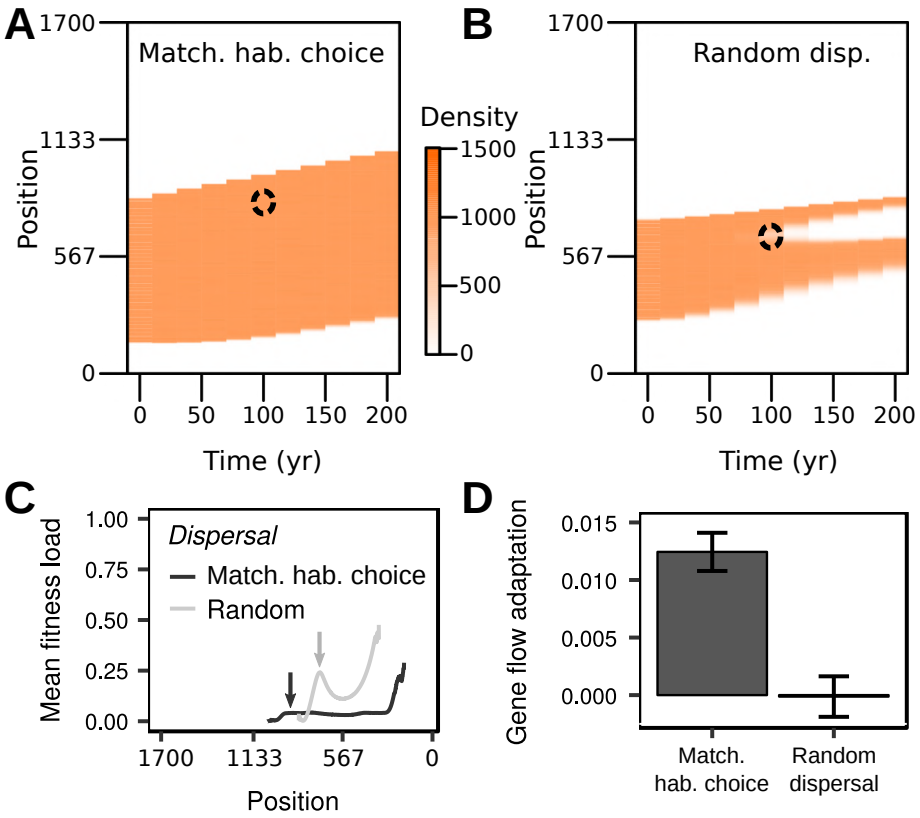

Figure S4.7 – Range fragmentation and associated gene flows. A,B) Populations density through space and time in case of matching habitat choice (A) and random dispersal (B). Solid lines represent the shift of the initial climatic niche of the species. Dashed circles represent the position in space and time at which D was taken. C) Local mean thermal fitness load (i.e. local maldaptation level) after 100 years of warming (1°C/100 years) in case of matching habitat choice (gray line) or random dispersal (black line). Arrow points in the space position delimited by dashed circles on A and B. D) Gene flow adaptation (see Methods) after 100 years of warming (1°C/100 years) behind the colonizing front (delimited by dashed circles on A and B) in case of matching habitat choice or random dispersal. Figures were taken for simulations under a warming of 1°C/100 years and a dispersal distance of 3 space units. A and B were drawn from a single simulation representative of others. In C, means over 50 simulations are shown. In D, means (±SD) over 50 simulations are shown.

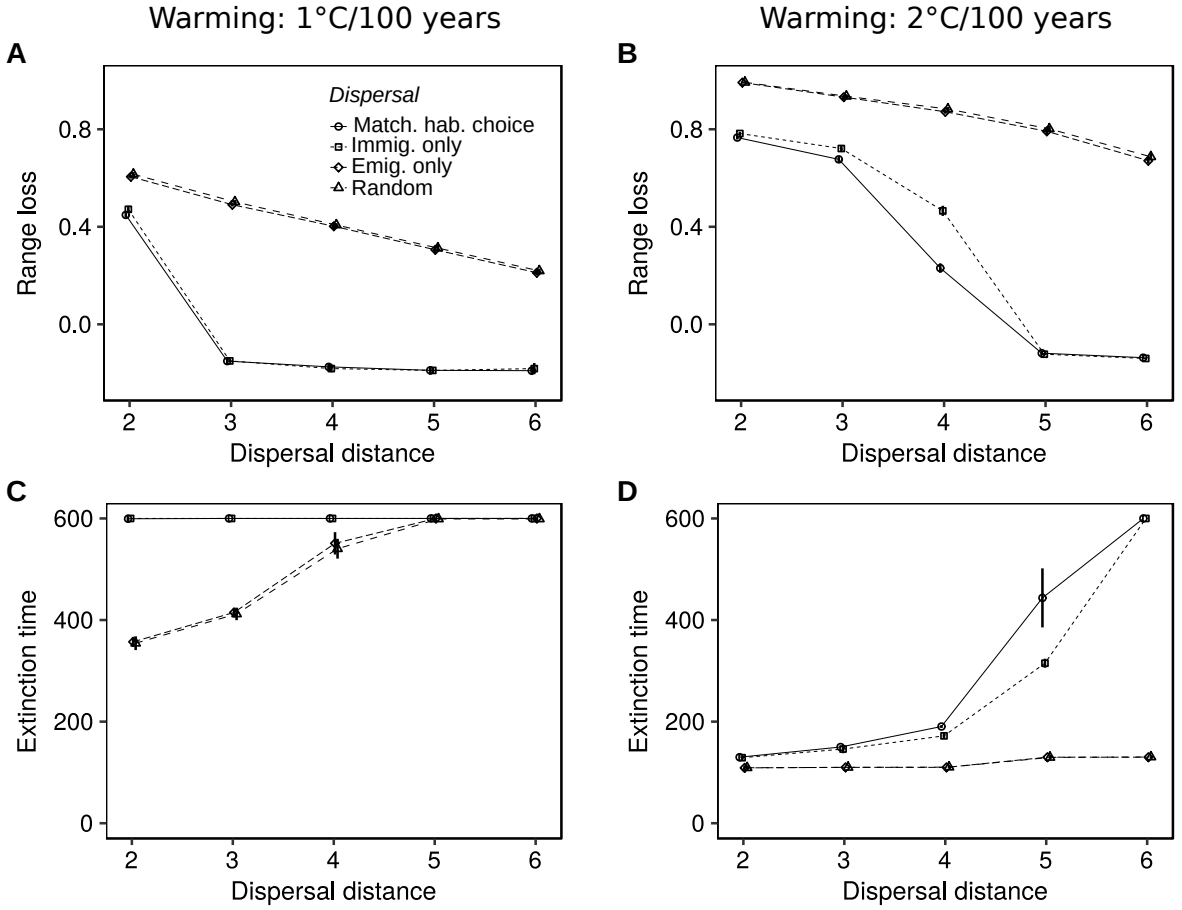

Figure S4.8 – Relative influence of adaptive immigration and adaptive emigration on species responses to climate change. Proportion of spatial range loss (A,B) and extinction time (C,D) depending on dispersal distance for matching habitat choice (adaptive immigration and adaptive emigration; circles and solid lines), adaptive immigration only (squares and dotted lines), adaptive emigration only (diamonds and dashed lines) or random dispersal (triangles and dashed lines) and for two climate change scenarios (scenario A,C: 1°C/100 years, scenario B,D: 2°C/100 years). Spatial range loss was measured after 200 years for scenario A and after 100 years for scenario B. When the species persisted until the end of simulations (600 years), the extinction time was indicated as 600 years. Means (± SD) over 50 (matching habitat choice and random dispersal) or 20 (adaptive immigration and adaptive emigration) simulations are shown.

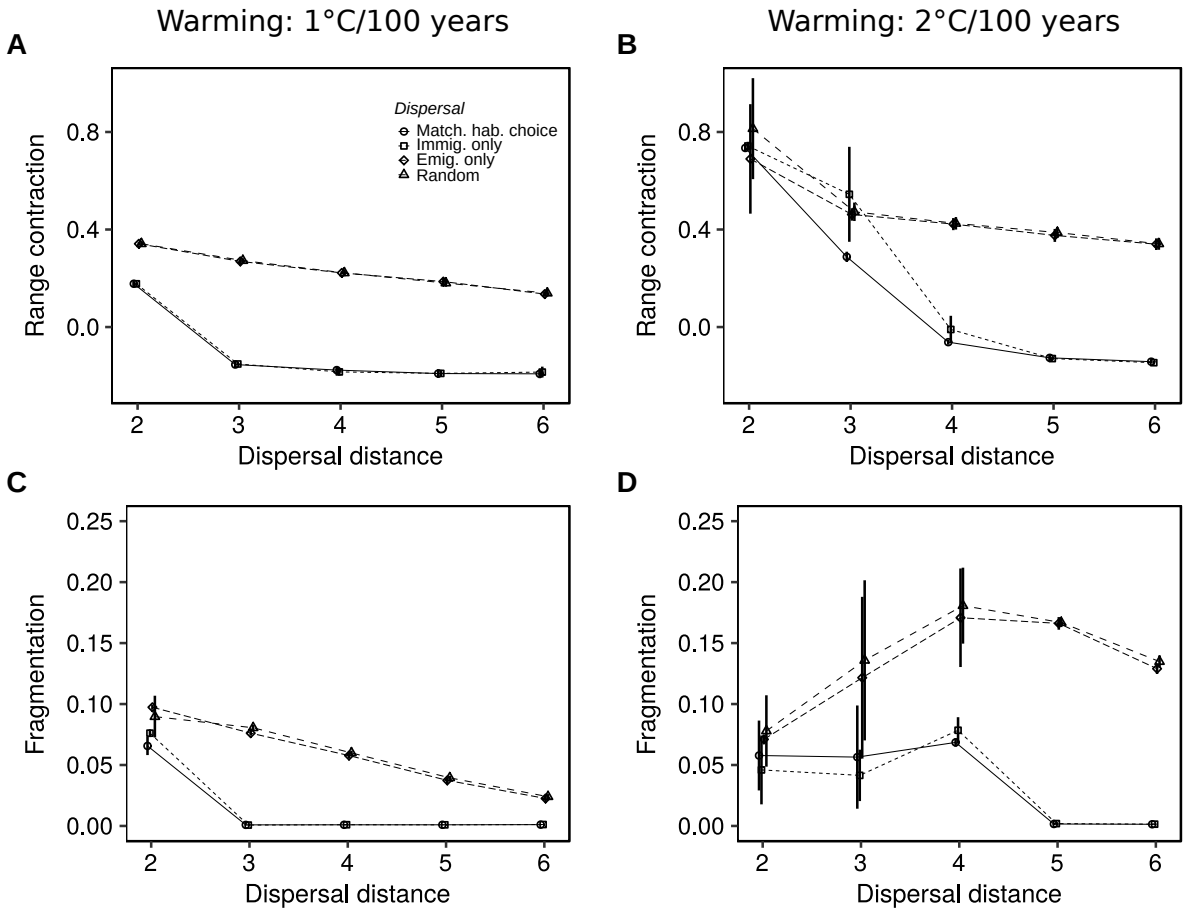

Figure S4.9 – Relative influence of adaptive immigration and adaptive emigration on spatial range contraction and fragmentation. Proportion of spatial range contraction (A,C) and spatial range fragmentation (B,D) depending on dispersal distance for matching habitat choice (adaptive immigration and adaptive emigration; circles and solid lines), adaptive immigration only (squares and dotted lines), adaptive emigration only (diamonds and dashed lines) or random dispersal (triangles and dashed lines) and for two climate change scenarios (scenario A,C: 1°C/100 years, scenario B,D: 2°C/100 years). Spatial range contraction was measured after 200 years for scenario A and after 100 years for scenario B. Spatial range fragmentation was measured between 0 and 200 years for scenario C and between 0 and 100 years for scenario D. Means (± SD) over 50 (matching habitat choice and random dispersal) or 20 (adaptive immigration and adaptive emigration) simulations are shown.

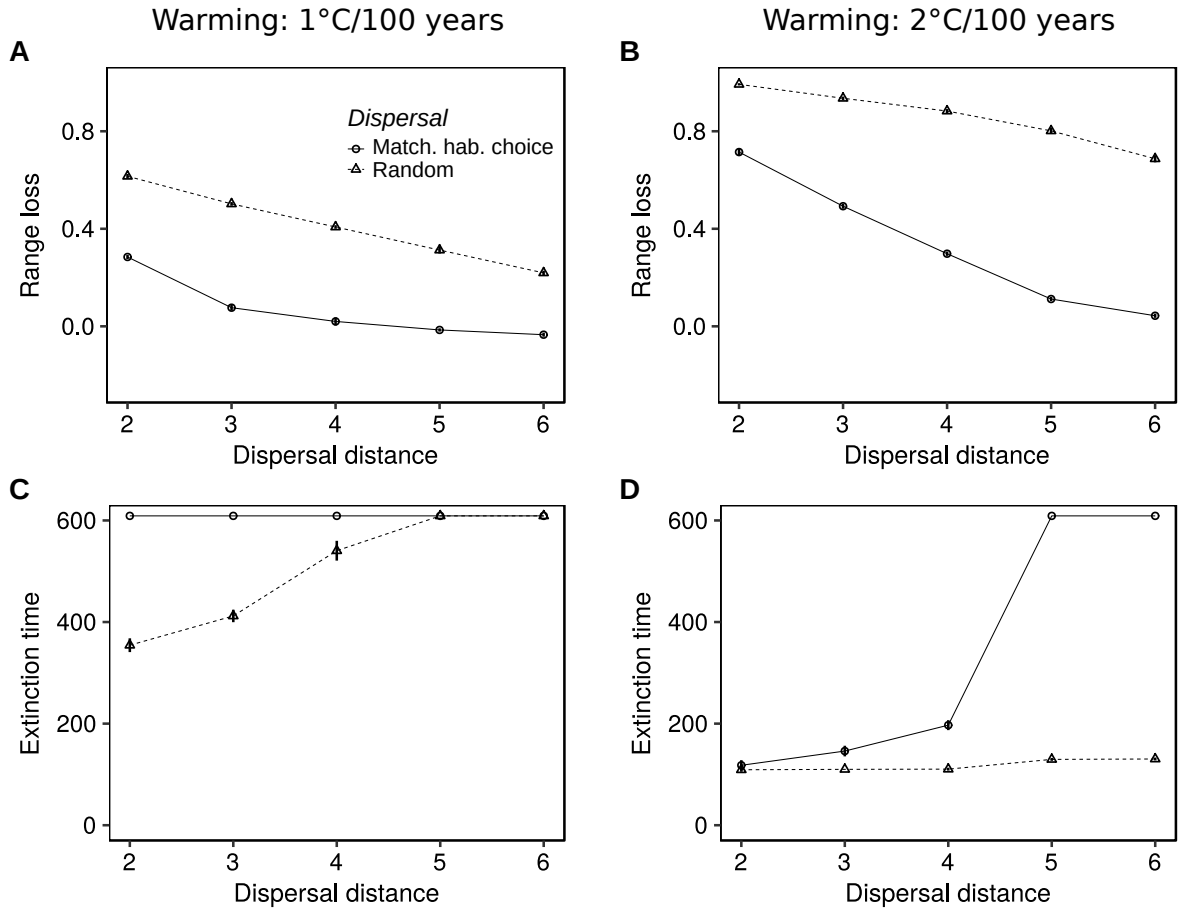

Figure S4.10 – Influence of density- and temperature- in matching habitat choice on species responses to climate change. Same as Figure 4.2 but for matching habitat choice depending on both temperature and density: proportion of spatial range loss (A,B) and extinction time (C,D) depending on dispersal distance in case of matching habitat choice depending on temperature and density (circles and solid lines) or random dispersal (triangles and dashed lines) and for two climate change scenarios (scenario A,C: 1°C/100 years, scenario B,D: 2°C/100 years). Spatial range loss was measured after 200 years for scenario A and after 100 years for scenario B. When extinction time reached 600 years, the species persisted until the end of the simulations. Means (± SD) over 50 (random dispersal) or 20 (matching habitat choice depending on temperature and density) simulations are shown.

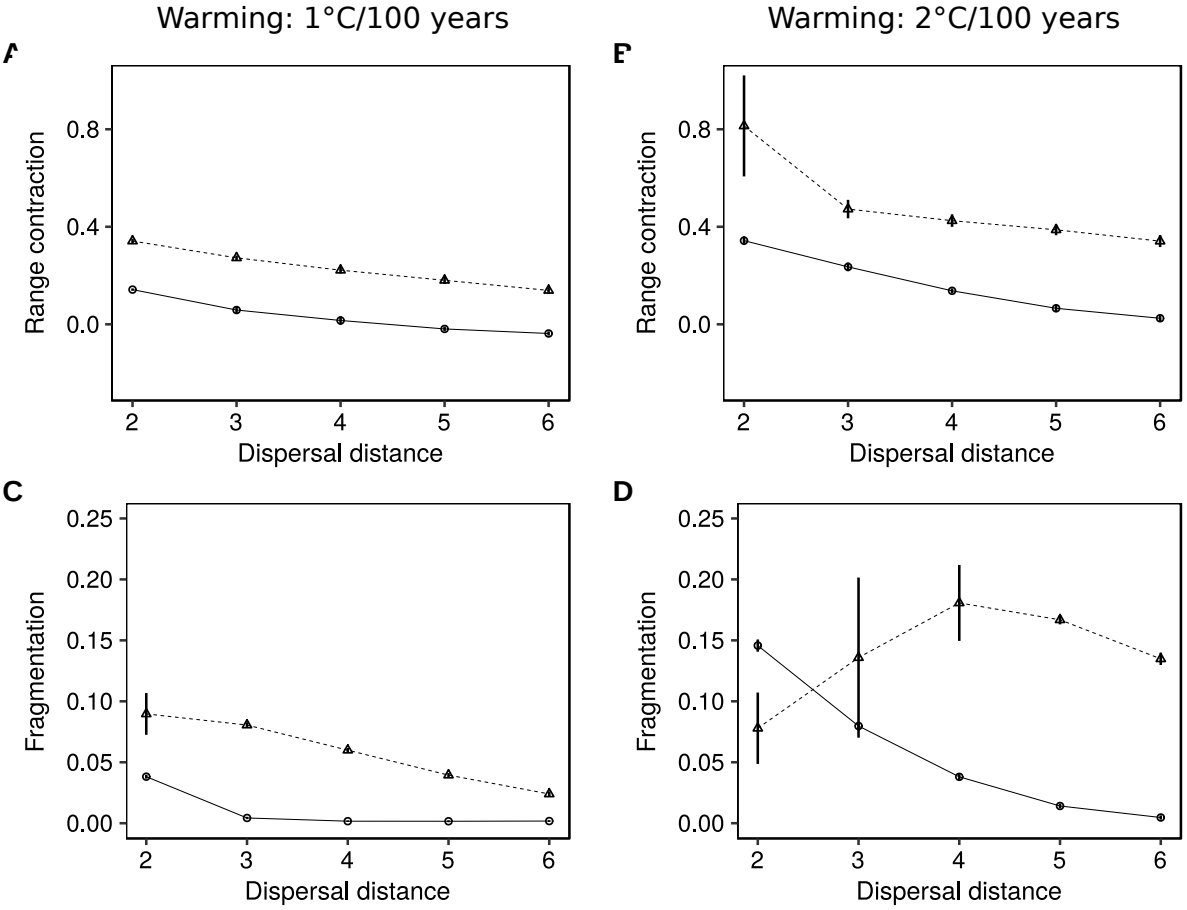

Figure S4.11 – Influence of density- and temperature- in matching habitat choice on spatial range contraction and fragmentation. Same as Figure 4.3 but for matching habitat choice depending on both temperature and density: proportion of spatial range contraction (A,C) and spatial range fragmentation (B,D) depending on dispersal distance in case of matching habitat choice depending on temperature and density (circles and solid lines) or random dispersal (triangles and dashed lines) and for two climate change scenarios (scenario A,C: 1°C/100 years, scenario B,D: 2°C/100 years). Spatial range contraction was measured after 200 years for scenario A and after 100 years for scenario B. Spatial range fragmentation was measured between 0 and 200 years for scenario C and between 0 and 100 years for scenario D. Means (± SD) over 50 (random dispersal) or 20 (matching habitat choice depending on temperature and density) simulations are shown.

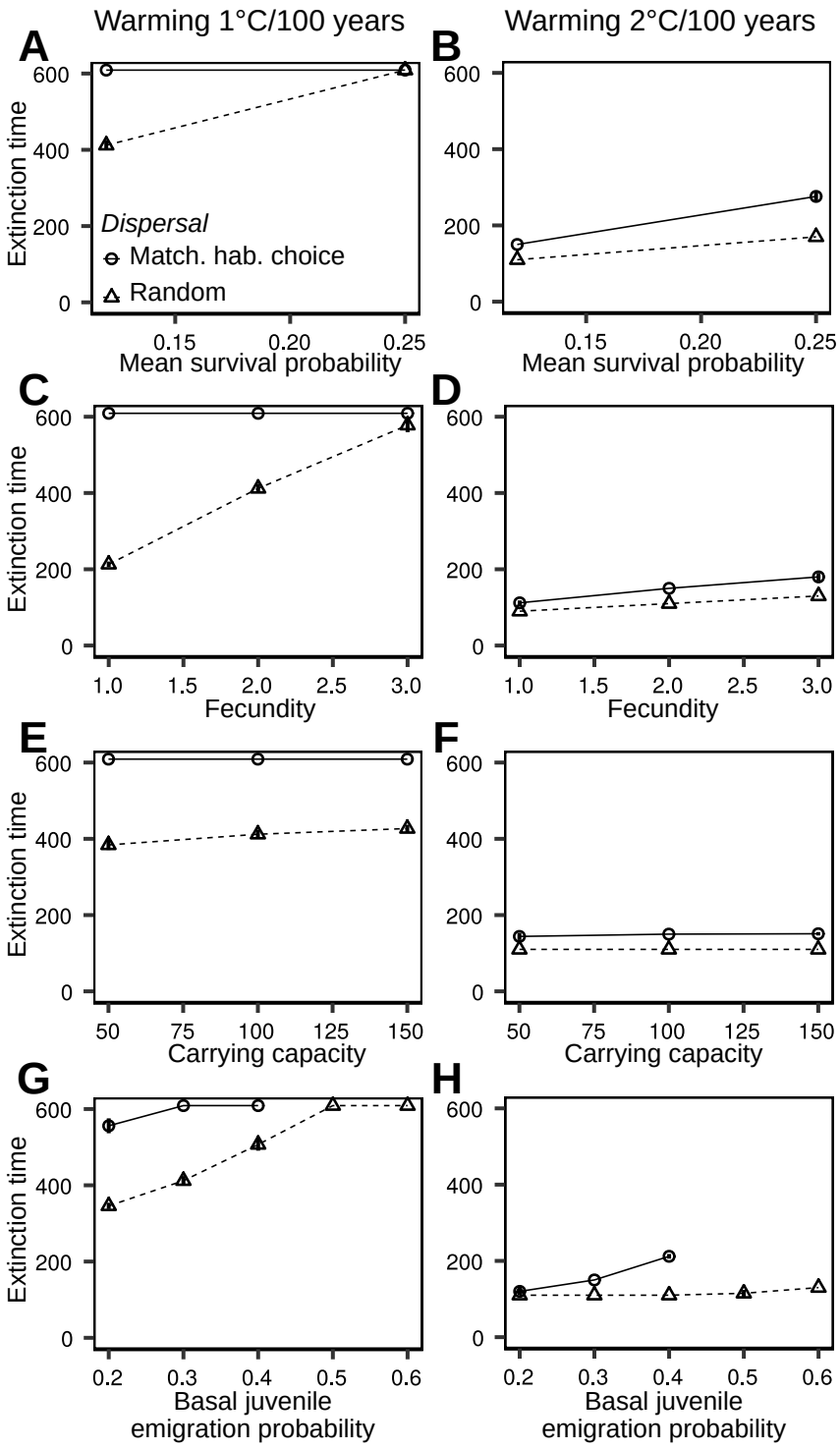

Figure S4.12 – Influence of demographic parameters on species extinction time facing climate change. Extinction time depending on survival probability (A,B), fecundity (C,D), carrying capacity (E,F) and emigration probability (G,H) in case of matching habitat choice (open circle, solid line) or random dispersal (open triangle, dashed line) and for two climate change scenarios (scenario A,C,E,G: 1°C/100 years, scenario B,D,F,H: 2°C/100 years). When extinction time reached 600 years, the species persisted until the end of the simulations. See section "Legend details" in supplementary materials for additional information. Means (± SD) over 50 (parameter values of main simulations (Table 4.1)) or 20 (parameter values of extra simulations (Table 4.1)) simulations are shown.

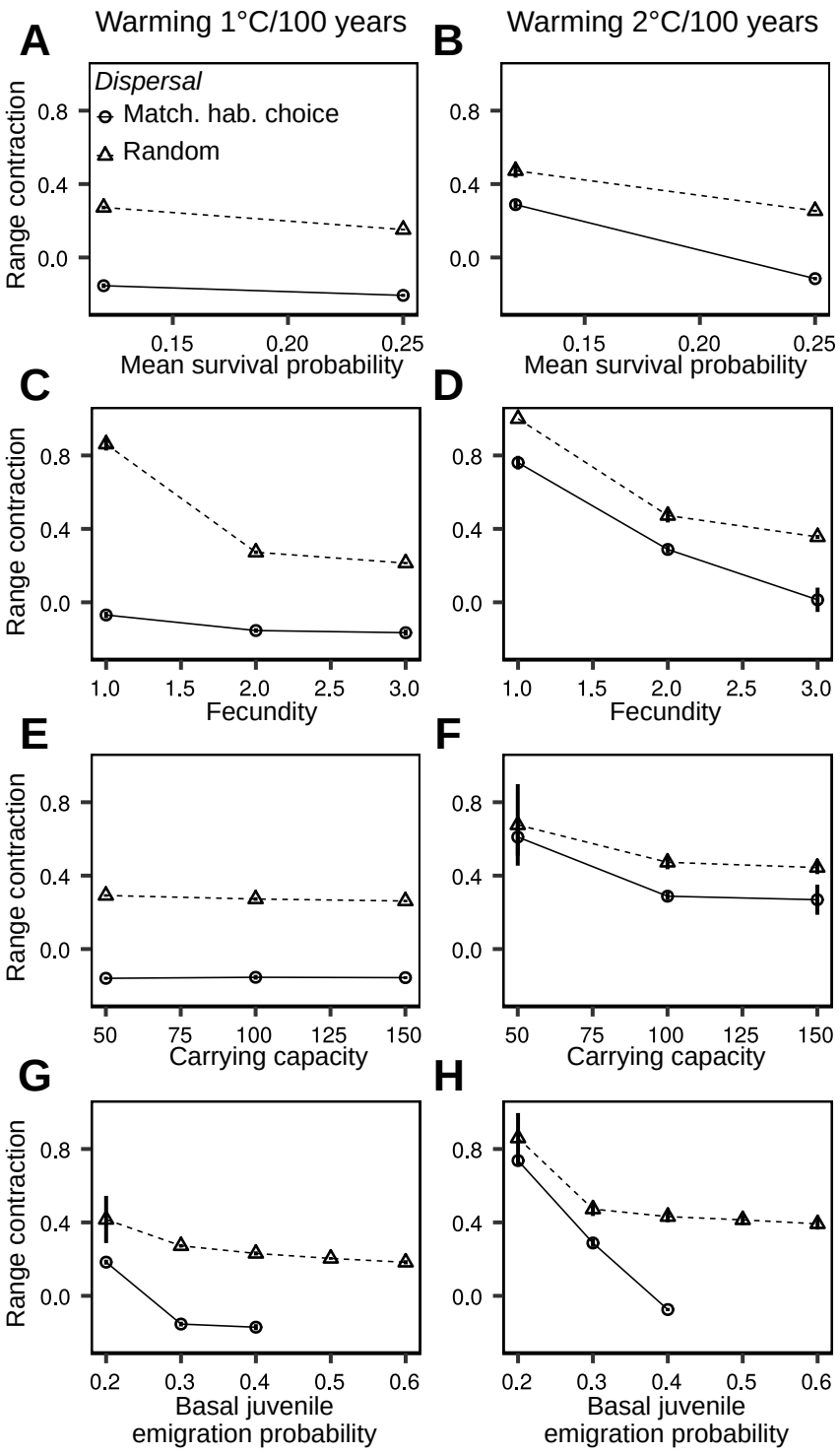

Figure S4.13 – Influence of demographic parameters on spatial range contraction during climate change. Spatial range contraction depending on survival probability (A,B), fecundity (C,D), carrying capacity (E,F) and emigration probability (G,H) in case of matching habitat choice (open circle, solid line) or random dispersal (open triangle, dashed line) and for two climate change scenarios (scenario A,C,E,G: 1°C/100 years, scenario B,D,F,H: 2°C/100 years). Spatial range contraction was measured after 200 years for scenario A,C,E,G and after 100 years for scenario B,D,F,H. See section "Legend details" in supplementary materials for additional information. Means (± SD) over 50 (parameter values of main simulations (Table 4.1)) or 20 (parameter values of extra simulations (Table 4.1)) simulations are shown.

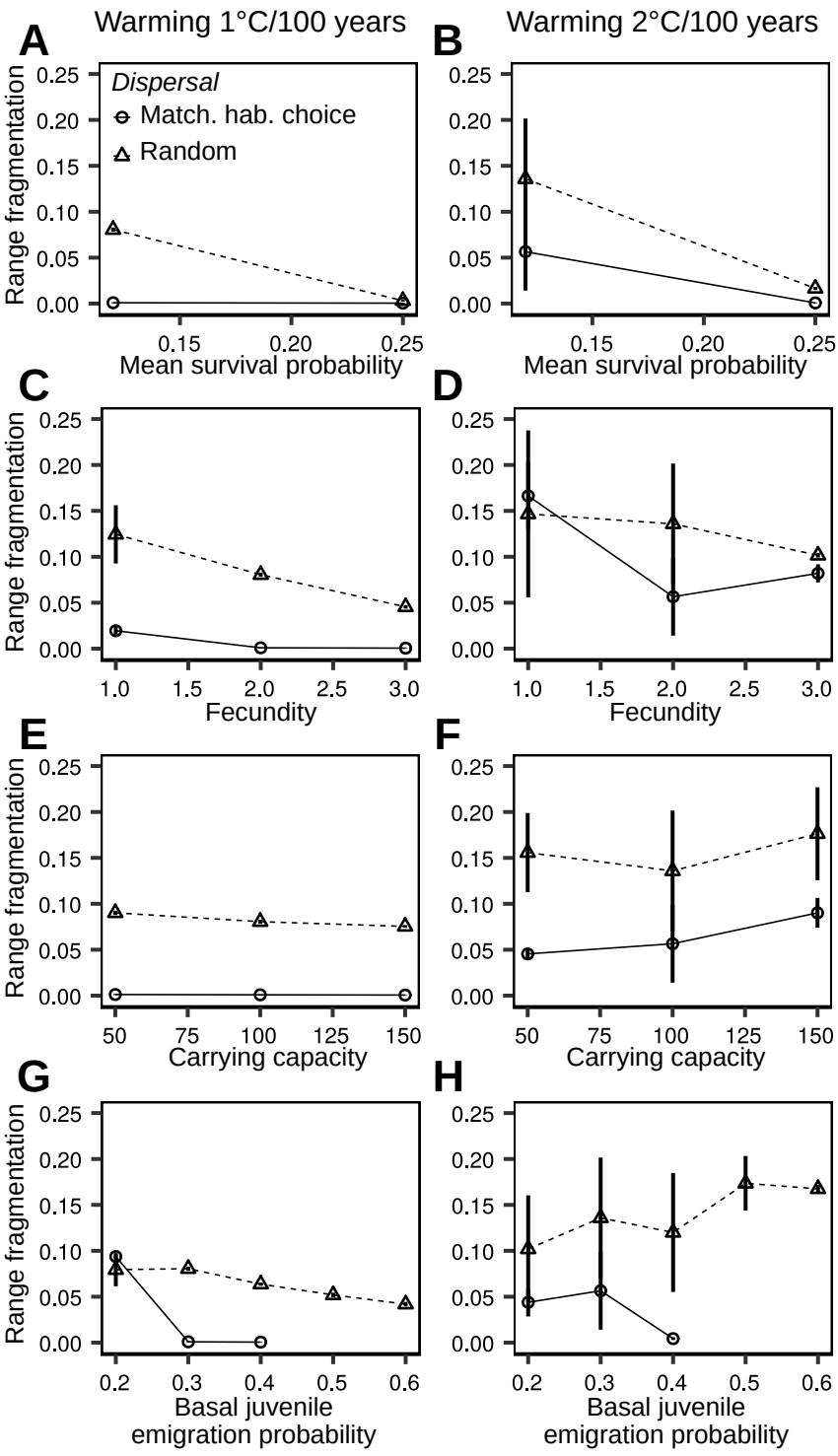

Figure S4.14 – Influence of demographic parameters on spatial range fragmentation during climate change. Spatial range fragmentation depending on survival probability (A,B), fecundity (C,D), carrying capacity (E,F) and emigration probability (G,H) in case of matching habitat choice (open circle, solid line) or random dispersal (open triangle, dashed line) and for two climate change scenarios (scenario A,C,E,G: 1°C/100 years, scenario B,D,F,H: 2°C/100 years). Spatial range fragmentation was measured between 0 and 200 years for scenario A,C,E,G and between 0 and 100 years for scenario B,D,F,H. See section "Legend details" in supplementary materials for additional information. Means (± SD) over 50 (parameter values of main simulations (Table 4.1)) or 20 (parameter values of extra simulations (Table 4.1)) simulations are shown.

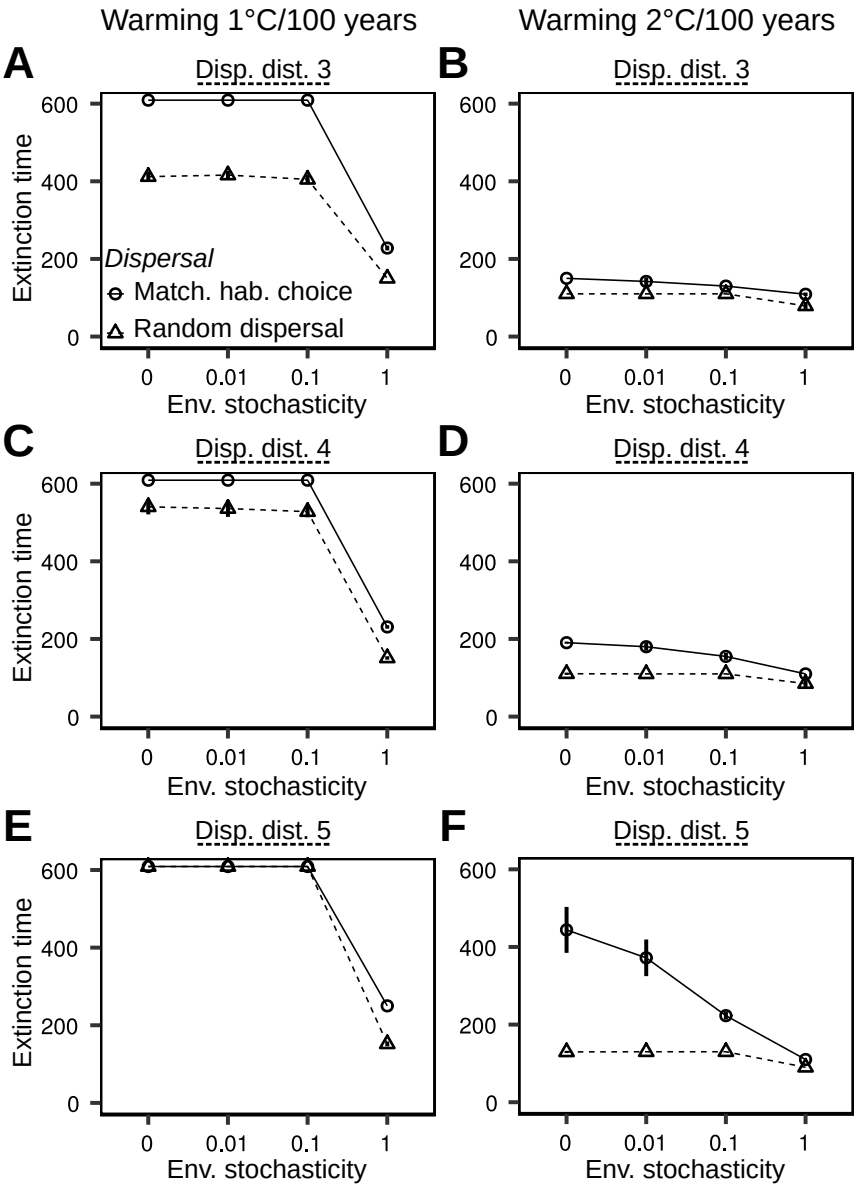

Figure S4.15 – Influence of environmental stochasticity on extinction time facing climate change. Extinction time depending on environmental stochasticity in case of matching habitat choice (circles and solid lines) or random dispersal (triangles and dashed lines) for different dispersal distances (A,B: 3 space units; C,D: 4 space units; E,F: 5 space units) and for two climate change scenarios (scenario A,C,E: 1°C/100 years, scenario B,D,F: 2°C/100 years). When extinction time reached 600 years, the species persisted until the end of the simulations. Means (± SD) over 50 (parameter values of main simulations (Table 4.1)) or 20 (parameter values of extra simulations (Table 4.1)) simulations are shown. Overall the results were the same as in Figure 4.6: Extinction time was always higher or the same in case of matching habitat choice than in case of random dispersal. Environmental stochasticity had a negative influence on extinction time.

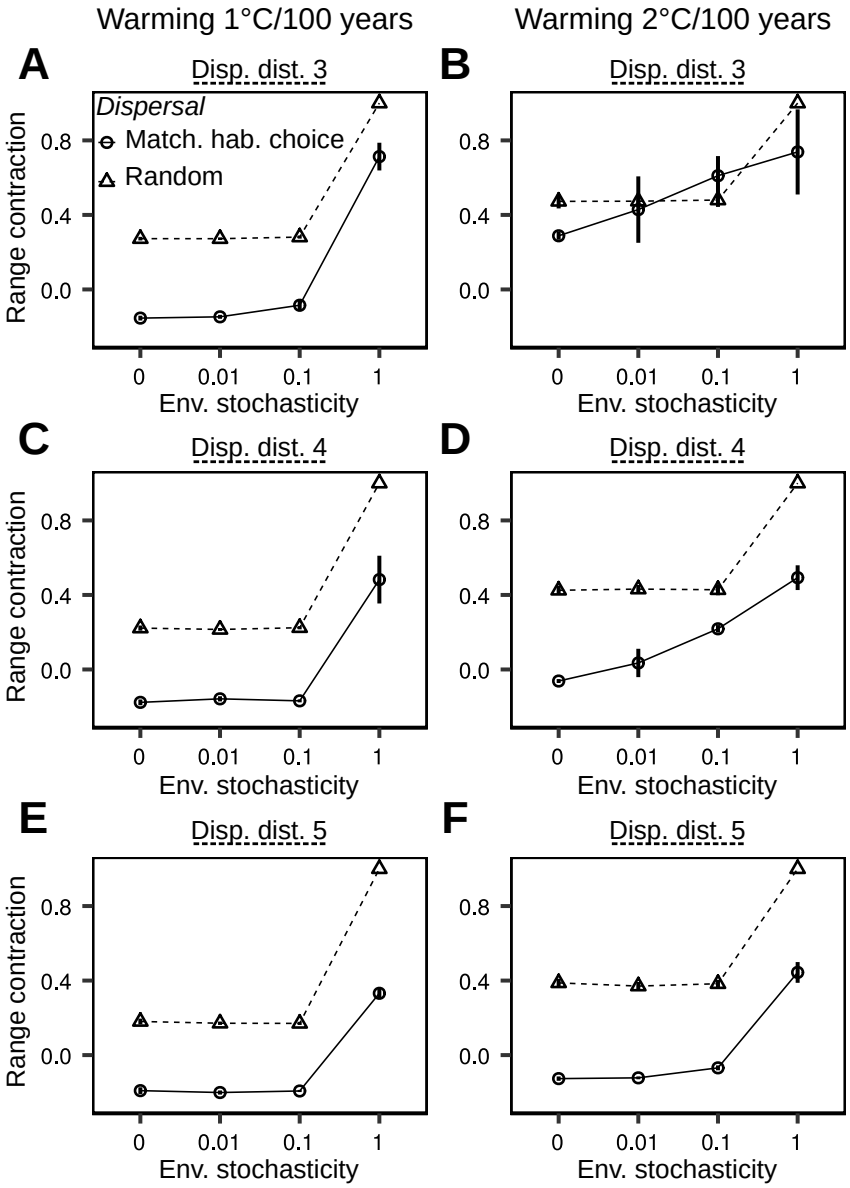

Figure S4.16 – Influence of environmental stochasticity on spatial range contraction during climate change. Spatial range contraction depending on environmental stochasticity in case of matching habitat choice (circles and solid lines) or random dispersal (triangles and dashed lines) for different dispersal distances (A,B: 3 space units; C,D: 4 space units; E,F: 5 space units) and for two climate change scenarios (scenario A,C,E: 1°C/100 years, scenario B,D,F: 2°C/100 years). Spatial range contraction was measured after 200 years for scenario A,C,E and after 100 years for scenario B,D,F. Means (± SD) over 50 (parameter values of main simulations (Table 4.1)) or 20 (parameter values of extra simulations (Table 4.1)) simulations are shown. Overall the results were the same as in Figure 4.6 and Figure S4.15: Range contraction was almost always lower in case of matching habitat choice than in case of random dispersal (excepted for a dispersal distance of 3 space units, a warming of 2°C/100 years and an environmental stochasticity of 0.1). Environmental stochasticity had a positive influence on spatial range contraction.

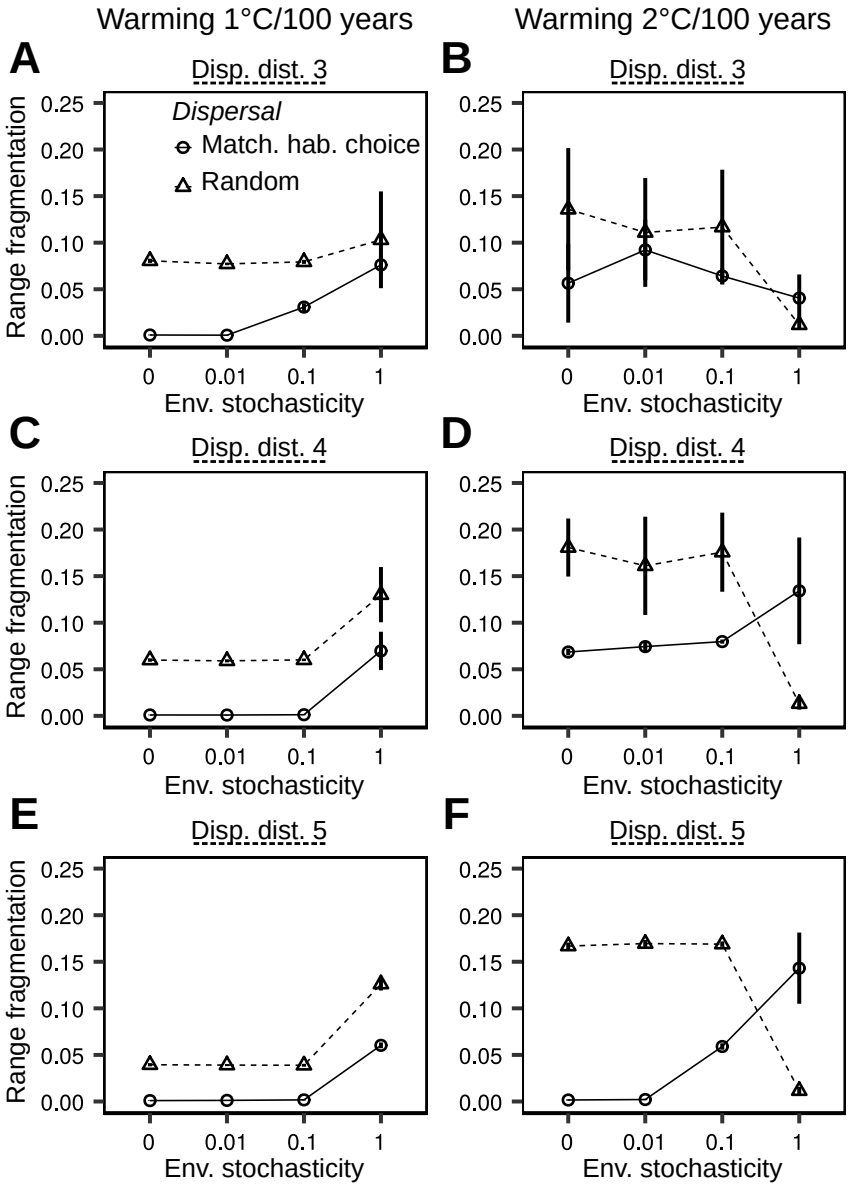

Figure S4.17 – Influence of environmental stochasticity on spatial range fragmentation during climate change. Spatial range fragmentation depending on environmental stochasticity in case of matching habitat choice (circles and solid lines) or random dispersal (triangles and dashed lines) for different dispersal distances (A,B: 3 space units; C,D: 4 space units; E,F: 5 space units) and for two climate change scenarios (scenario A,C,E: 1°C/100 years, scenario B,D,F: 2°C/100 years). Spatial range fragmentation was measured between 0 and 200 years for scenario A,C,E and between 0 and 100 years for scenario B,D,F. Means (± SD) over 50 (parameter values of main simulations (Table 4.1)) or 20 (parameter values of extra simulations (Table 4.1)) simulations are shown. See section "Legend details" in supplementary materials for interpretation.

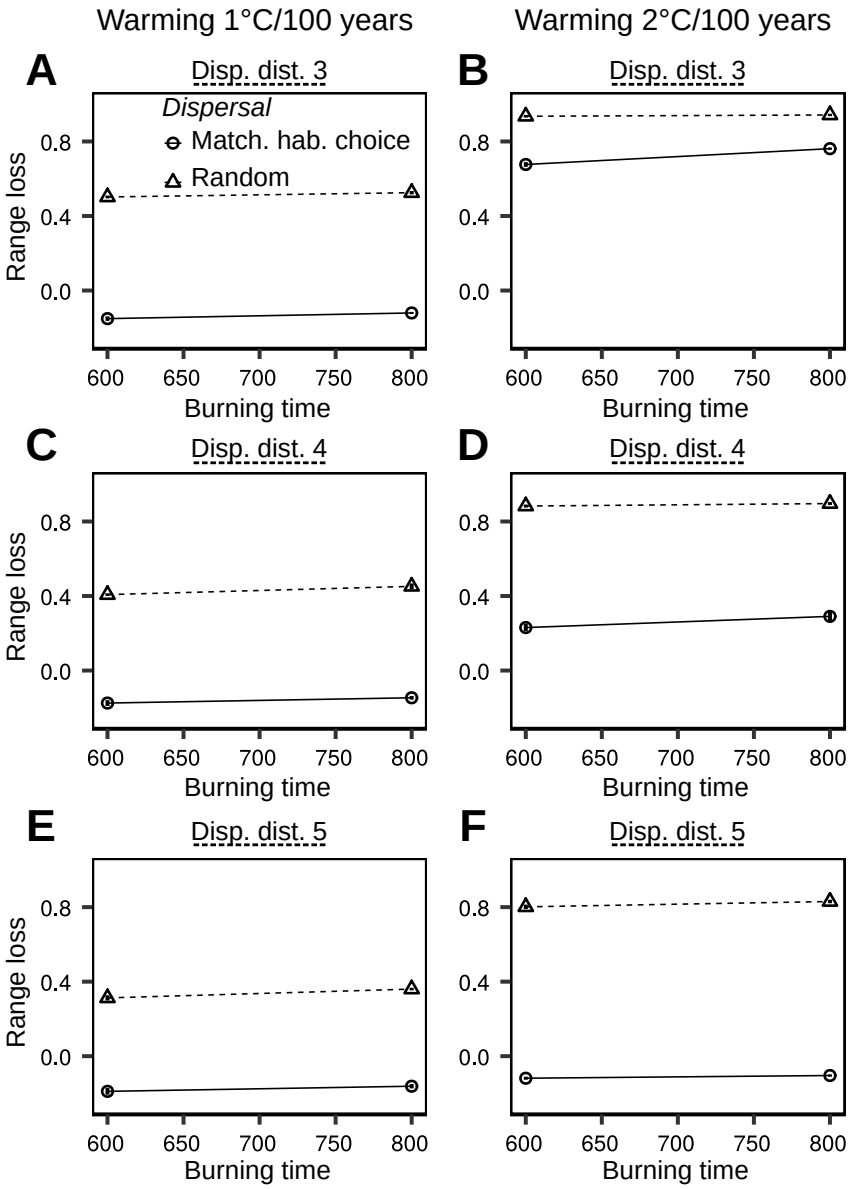

Figure S4.18 – Influence of burning time spatial range loss during climate change. Proportion of spatial range loss depending on time of stable climate before the period of climate change in case of matching habitat choice (circles and solid lines) or random dispersal (triangles and dashed lines) for different dispersal distances (A,B: 3 space units; C,D: 4 space units; E,F: 5 space units) and for two climate change scenarios (scenario A,C,E: 1°C/100 years, scenario B,D,F: 2°C/100 years). Spatial range loss was measured after 200 years of warming for scenario A,C,E and after 100 years of warming for scenario B,D,F. Means (± SD) over 50 (parameter values of main simulations (Table 4.1)) or 20 (parameter values of extra simulations (Table 4.1)) simulations are shown.

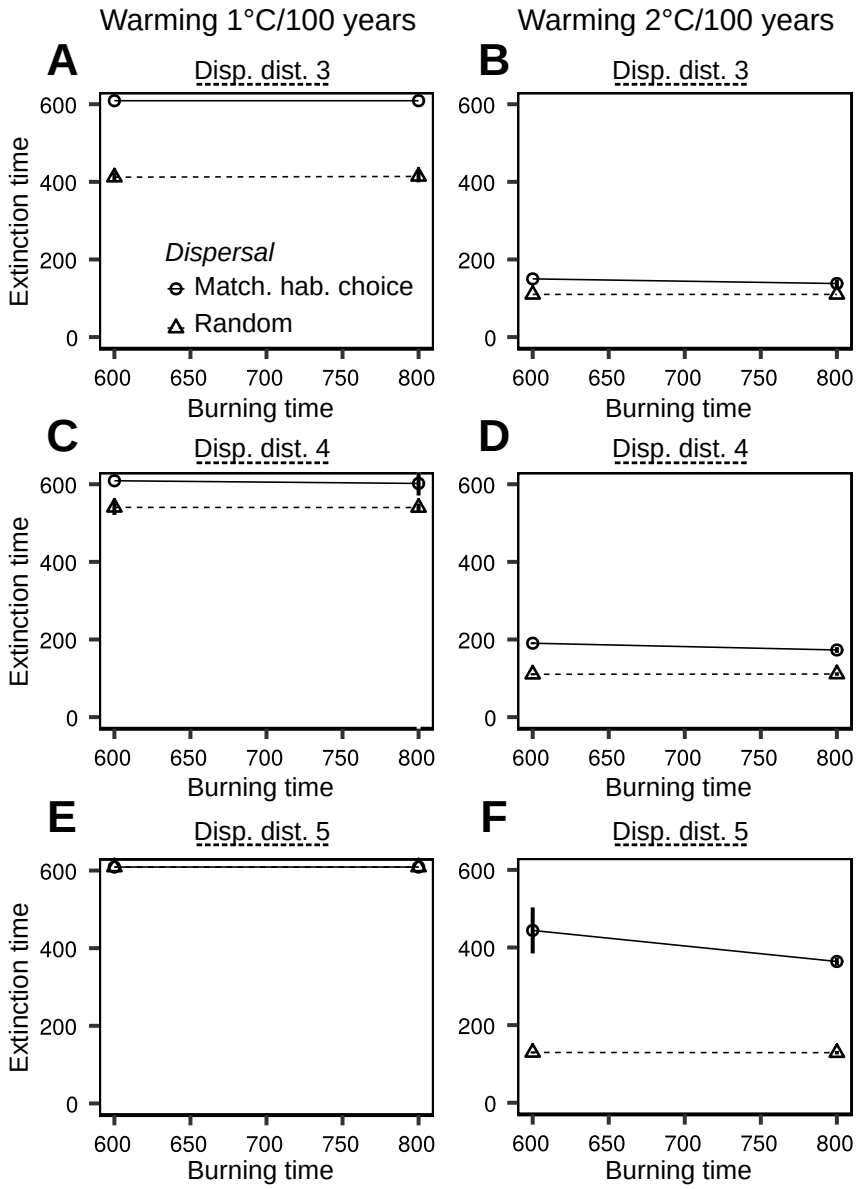

Figure S4.19 – Influence of burning time on extinction time facing climate change. Extinction time depending on time of stable climate before the period of climate change in case of matching habitat choice (circles and solid lines) or random dispersal (triangles and dashed lines) for different dispersal distances (A,B: 3 space units; C,D: 4 space units; E,F: 5 space units) and for two climate change scenarios (scenario A,C,E: 1°C/100 years, scenario B,D,F: 2°C/100 years). When extinction time reached 600 years, the species persisted until the end of the simulations. Means (± SD) over 50 (parameter values of main simulations (Table 4.1)) or 20 (parameter values of extra simulations (Table 4.1)) simulations are shown.

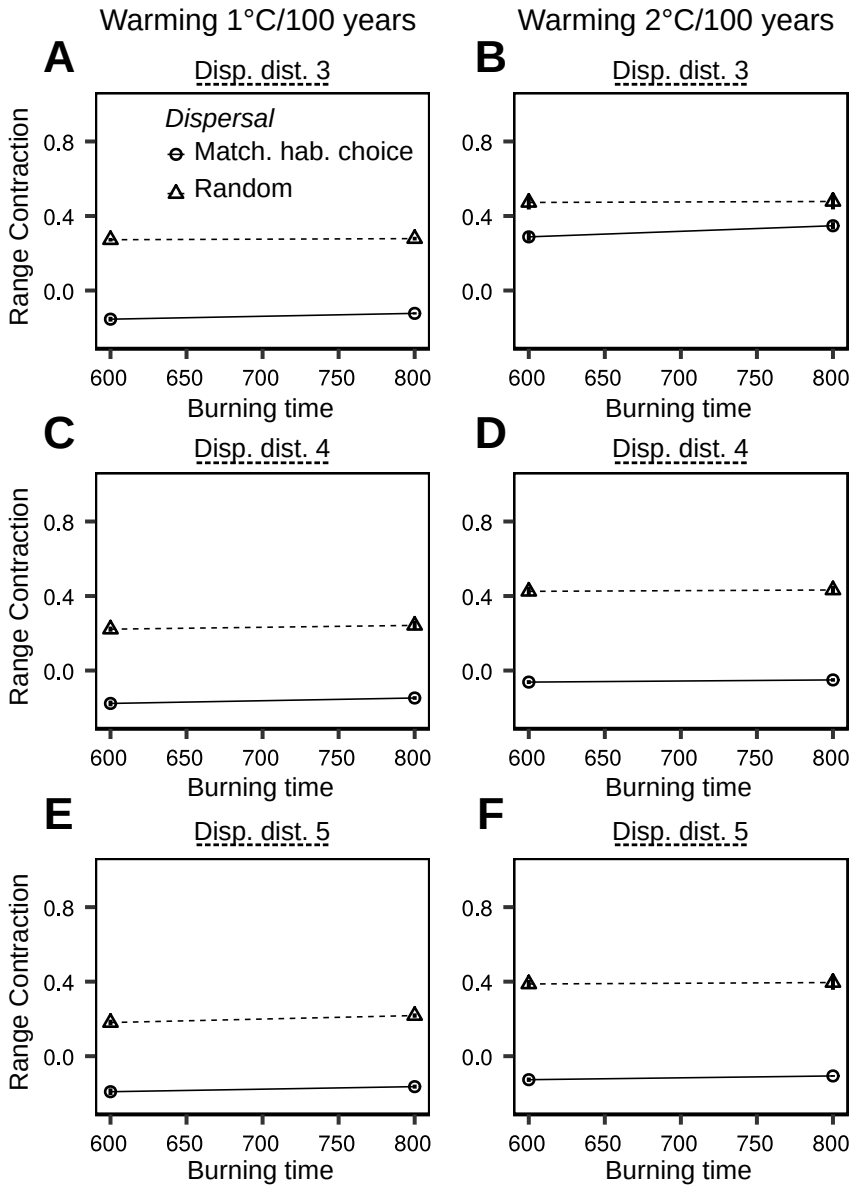

Figure S4.20 – Influence of burning time on spatial range contraction during climate change. Spatial range contraction depending on time of stable climate before the period of climate change in case of matching habitat choice (circles and solid lines) or random dispersal (triangles and dashed lines) for different dispersal distances (A,B: 3 space units; C,D: 4 space units; E,F: 5 space units) and for two climate change scenarios (scenario A,C,E: 1°C/100 years, scenario B,D,F: 2°C/100 years). Spatial range contraction was measured after 200 years for scenario A,C,E and after 100 years for scenario B,D,F. Means (± SD) over 50 (parameter values of main simulations (Table 4.1)) or 20 (parameter values of extra simulations (Table 4.1)) simulations are shown.

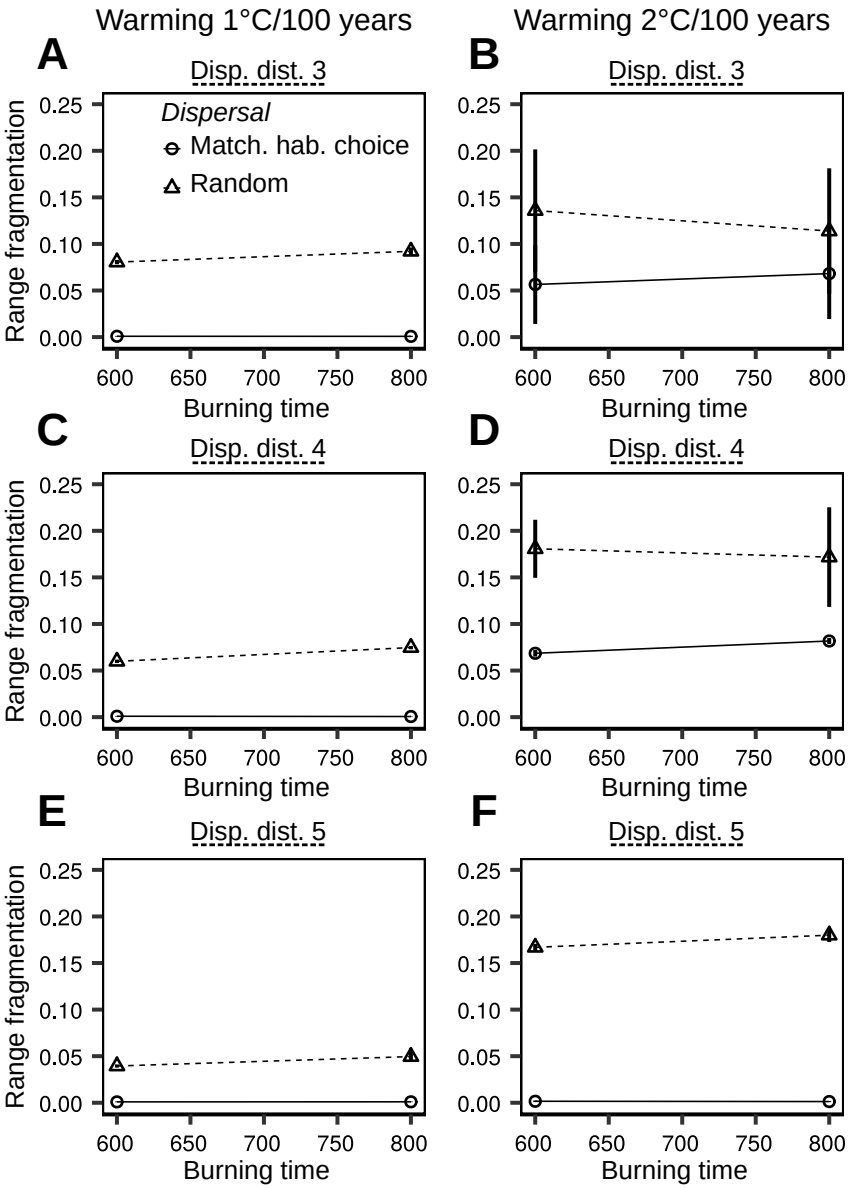

Figure S4.21 – Influence of burning time on spatial range fragmentation during climate change. Spatial range fragmentation depending on time of stable climate before the period of climate change in case of matching habitat choice (circles and solid lines) or random dispersal (triangles and dashed lines) for different dispersal distances (A,B: 3 space units; C,D: 4 space units; E,F: 5 space units) and for two climate change scenarios (scenario A,C,E: 1°C/100 years, scenario B,D,F: 2°C/100 years). Spatial range fragmentation was measured between 0 and 200 years for scenario A,C,E and between 0 and 100 years for scenario B,D,F. Means (± SD) over 50 (parameter values of main simulations (Table 4.1)) or 20 (parameter values of extra simulations (Table 4.1)) simulations are shown.

5 General Discussion

1 Discussion

The common method used in science to tackle a specific question, or to understand a biological system, is to start with the simplest scenario and to gradually add complexity in the system. The simplest scenario will be used as a reference to compare results obtained with a more complex scenario. This gradual approach enables to isolate the influence of parameters or mechanisms added at each step of the complication process. Then, when isolated and fully understood, each mechanism can be modeled to extrapolate its influence on larger spatio-temporal scales. This step by step approach has been used as a guideline for this PhD. In our experimental system (Chapters 2 and 3), the simplest scenario was the pairs of isolated enclosures, one with a present-day climate and the other with a warm climate. This simple scenario measures population responses to different climatic conditions excluding the influence of dispersal. Then, the scenario with connected enclosures was compared to this "simple" scenario to explore how dispersal, in its complex rules, modulate other processes shaping population responses to climate change. Then, we integrated dispersal, as we observed it in our experiment, into a theoretical model to predict its influence on population responses to climate change on the whole geographical distribution of the species, over hundreds of year. The same logic has been used in the following discussion.

The aim of this thesis was to better understand how populations respond to climate

change and how dispersal and landscape structure modulate these responses, thanks to a combination of experimental and modeling approaches. We found that climate change affected population age structure and population mean body size by accelerating individual pace of life (Chapter 2). Individuals had a faster growth rate and reproduced earlier under warm climatic conditions while adult survival was reduced. Phenotypic composition of the population was also affected by the climatic conditions; after three years of climatic treatment, individuals living in warm climatic conditions were paler than individuals living in present-day climatic conditions (Chapter 3). Phenotypic differentiation was mainly due to phenotypic plasticity. However, we found a strong influence of landscape structure on population response to climate change. When populations were connected, individuals could disperse from one climatic condition to another. The influence of climate change on population dynamics and population phenotypic composition was buffered by this flow of individuals. Indeed, we did not observe climatic effect on population age structure and on population phenotypic composition in connected populations. We observed that dispersal was non random regarding individual characteristics and climatic conditions. The flow of individuals was biased from present-day climate to warm climate. Moreover, dispersal was adaptive and driven by the match between individual phenotype and local temperature. Non-random dispersal affected population density and enhanced selective pressures acting on phenotypes. The relative roles of phenotypic plasticity and evolutionary adaptation were thus determined by dispersal. On a larger spatio-temporal scale, we found that non-random dispersal, in particular matching habitat choice that we observed in our experiments, strongly affected species persistence under climate change (Chapter 4). When considered into predictive models, matching habitat choice promoted species range shift and reduced population extinction risk under climate change.

In isolated conditions (i.e. without dispersal), populations inhabiting warmer climatic conditions for three years differed from populations inhabiting present-day climatic conditions regarding both their dynamics and their phenotypic composition. Populations in warmer climate were indeed composed of younger, larger and paler individuals than those composing populations in present-day climate. Changes in population dynamics and phe-

notypic composition may interact with each other to shape the general response to climate change. In an eco-evolutionary feedback loop (Le Galliard *et al.*, 2005a; Kokko & López-Sepulcre, 2007; Schoener, 2011), demographic and ecological processes affect evolution and vice versa. In our system, the climate-related change in population age structure might have driven population phenotypic change. We observed that the proportion of young individuals increased in warm conditions. If selection on particular phenotypic traits act mostly on younger age classes, evolutionary phenotypic change might be enhanced by the change in population age structure that increase the density of young individuals. Conversely, if selective pressures act mainly on the adult stage, then evolutionary changes would be hampered by the global decrease in adult survival. On the other hand, changes in population phenotypic composition may also affect population dynamics. If particular phenotypes have selective advantage over others, they could thus be more competitive, have easier access to resources, grow faster and thus reproduce earlier, enhancing the decrease in population mean age. From a broader point of view, phenotypic distribution could correlate with life history strategies. In the commonly used r to K pace of life continuum (Pianka, 1970), some phenotypic traits could be associated with the different strategies (e.g. thermal type, Goulet *et al.*, 2017). Climate-related changes regarding phenotypes may thus lead to changes in population dynamics. In the present study, the effect of the climatic treatment on adult dorsal darkness was still present when controlling for individual age and body size, meaning that change in population phenotypic composition was not directly caused by the change in age structure. However, we did not explore the direct link between life history strategies and thermal phenotypes. Further analyses on our dataset could bring light on how climate change could favor thermal "type" or "syndrome" affecting both population dynamics and composition, rather than treating them as separate population responses.

Correlations between life-history traits and/or other phenotypic traits are also known to influence dispersal. Indeed, dispersers are often characterized by a combination of traits promoting movements, decreasing dispersal costs or increasing benefits of dispersal (i.e. dispersal syndromes (Clobert *et al.*, 2009; Ronce & Clobert, 2012; Cote *et al.*, 2017)).

Also, dispersal is driven by individual phenotypes (e.g. presence of wing), local conditions (e.g. conspecific density) and often their match (i.e. matching habitat choice (Bowler & Benton, 2005; Edelaar *et al.*, 2008)). In the first two chapters of this thesis, we demonstrated that dispersal was affected by the climatic condition (Chapter 2), the phenotype of the individuals (body size, Chapter 2) and the match between individual phenotype and the local climatic condition (body size/thermal preference in adults (Chapter 2 and 3), dorsal darkness in juvenile(Chapter 3)). Previous studies already demonstrated that in the common lizard (*Zootoca vivipara*), dispersal was affected by the local context (e.g. local density (Le Galliard *et al.*, 2005b), temperature (Massot *et al.*, 2008)) and the match between phenotype and local context (e.g. social behavior and local density (Cote & Clobert, 2007b), dorsal pattern and climatic conditions (Lepetz *et al.*, 2009), thermal preference and climatic condition (Bestion *et al.*, 2015a)). Matching habitat choices have already been demonstrated in numerous species and different phylogenetic groups (e.g. insects (Karpestam *et al.*, 2012), fishes (Bolnick *et al.*, 2009), birds (Dreiss *et al.*, 2012; Camacho *et al.*, 2016; Benkman, 2017), reptiles (Cote *et al.*, 2007, 2008); reviewed in Edelaar *et al.* (2008)). Despite these evidences, dispersal is often considered as a neutral and stochastic process (Lowe & McPeek, 2014). The three chapters of this thesis demonstrated that the complexity of dispersal is of central importance in population responses to new climatic conditions and to predict the future of biodiversity in the context of global change.

Indeed, dispersal had various consequences on population responses to climate change. We observed that dispersal buffered the influence of climatic conditions on population age structure and phenotypic composition. However, the movement of individuals between the two climatic conditions affected population density and modulate the relative influence of phenotypic plasticity and evolutionary adaptation in population phenotypic change. Indeed, dispersal modify the strength of selection on heritable traits, making response to selection possible ($R = S * h^2$, breeder equation, see Morrissey *et al.* (2010) for details and criticism). The observed effects on population dynamics and composition rely on the fact that dispersal was non-random. Dispersal buffered the impact of climate change on

age structure and induced demographic changes because of the biased flow from present-day climate populations to warmer climate populations. Climate-dependent dispersal creates a disequilibrium between emigration and immigration rates resulting in a source-sink system. Furthermore, the influence of phenotypic plasticity in driving phenotypic differentiation among climates was offset by matching habitat choice. Dispersal indeed (i) drove population phenotypic composition in the opposite direction of phenotypic plasticity and (ii) strengthened selective pressures on phenotypes also in the opposite direction of phenotypic plasticity. Whereas theory predicts that phenotypic plasticity should be promoted against evolutionary adaptation in presence of random dispersal (Sultan & Spencer, 2002), we experimentally demonstrated the opposite. Moreover, considering matching habitat choice when forecasting future species distribution under climate change strongly affected predictions. In a situation where matching habitat choice was perfect (i.e. individuals were able to choose the habitat that perfectly match their phenotype), we showed that predictions regarding the evolution of range size could be reversed; the model predicted important range contraction under random dispersal whereas species range was predicted to expand when matching habitat choice was considered. For a few decades, species distribution models (SDMs) have been the main used models to predict future species distribution under climate change (e.g. Bakkenes *et al.*, 2002; Thuiller *et al.*, 2005; Broennimann *et al.*, 2006; Schwartz *et al.*, 2006). Despite some improvements of these models, SDMs usually considered species as entities (i.e. ignored population differentiation and local adaptation), ignored biological interactions and either ignored dispersal or modeled it as random (Hampe, 2004). Here we highlighted the urgent need to consider dispersal as a complex and non random process.

Beside this, dispersal has been shown to evolve quickly (e.g. Phillips *et al.*, 2006; Legrand *et al.*, 2016). Dispersal is shaped by selection pressures link to biotic and abiotic factors such as population density (Simmons & Thomas, 2004; Massol *et al.*, 2011), kin competition (Rousset & Gandon, 2002), and landscape structure (Hill *et al.*, 1999; Hanski *et al.*, 2004; Schtickzelle *et al.*, 2006). Under climate change, dispersal could also evolve and modulate range expansion (Travis *et al.*, 2009; Bocedi & Travis, 2016). In the context

of global change, landscape fragmentation plays an important role on dispersal evolution. It is predicted that dispersal probability should be reduced in fragmented landscape due to the increase in dispersal cost associated with movements through unsuitable habitats (Travis *et al.*, 1999). However, the influence of landscape fragmentation on dispersal evolution could be more complex (e.g. see Schtickzelle *et al.*, 2006), making prediction of species response to climate change in an increasingly fragmented landscape hard to achieve (Bocedi *et al.*, 2014).

Throughout this thesis, I gave some new arguments/predictions on the potential influence of habitat fragmentation on species response to climate change. In the extreme situation where fragmentation was total and populations were totally isolated, we demonstrated that the effects of climate change on population dynamics and composition were strong compared to the situation of connected populations. On a larger scale, this extreme situation should surge species extinction under climate change. For example, Thomas *et al.* (2004) predicted the extinction of 26-37% of all species in 2050 with a mid-range climate change scenario in absence of dispersal (similar to a situation of total fragmentation preventing dispersal) whereas the extinction concerned "only" 15-20% of species when dispersal was allowed. However, such an extreme situation is not realistic. The process of fragmentation splits suitable habitats into a number of small and isolated patches (Wilcove *et al.*, 1986; Fahrig, 2003), reducing habitat surface and increasing the distance among patches. Despite being constrained, dispersal among patches is often maintained. In that case, the structure of the landscape is expected to play an important role as it should shape dispersal pattern and influence species range shift (McInerny *et al.*, 2007). Landscape structure could also directly influence dispersal in constraining individual movements. Indeed, habitat fragmentation may reduce the adaptive potential of gene flow in limiting the exploration of surrounding habitat by dispersers. Dispersal decisions thus should be non-optimal (Jacob *et al.*, 2015a; Cote *et al.*, 2017). We demonstrated in Chapter 4 that decreasing optimality in dispersal decision strongly affected species persistence compared to a situation where dispersal decisions were optimal. For that reason, we predicted landscape fragmentation to have an unexpectedly strong negative influence

on species persistence in the context of climate change. Whereas we argued that models predicting future species distribution might be too pessimistic in ignoring matching habitat choice, we think that landscape fragmentation might offset the benefice of adaptive dispersal, making current global change a "deadly anthropogenic cocktail" (Travis, 2003).

On a smaller scale, landscape fragmentation limits contacts between populations inhabiting different microclimates. Microclimates could be used very locally by the individuals to avoid overheating during heatwaves (Scheffers *et al.*, 2014; Suggitt *et al.*, 2018). It could also play the role of refuge area during periods of environmental perturbations such as climate change, allowing fast recolonization at the end of the perturbation (Pearson, 2006). Finally, microclimates are predicted to buffer the influence of climate change on biodiversity and reduce predictions of species extinction (Lenoir *et al.*, 2017; Lembrechts *et al.*, 2018). Indeed, whereas temperature should increase continuously through time at the global scale, climate change should not be homogenous at the local scale (Ashcroft *et al.*, 2009). Populations may benefit from these "cool" microclimates to persist. We experimentally demonstrated that microclimates indeed allowed to buffer the influence of climate change. However, it could be costly for population initially inhabiting cool microclimate (i.e. decreased density). As in classic source-sink dynamics, the continuous flow of individuals from the source population to the sink could unbalance the source populations and then the whole system (Gundersen *et al.*, 2001). However, adaptive dispersal could also promote adaptation to the warm microclimate. Moreover, refuges, when they are accessible, could allow individual and population persistence for longer period of time, letting time for genetic adaptation to happen. Further experiments manipulating climatic conditions in connected populations on longer period of time may help predict in which direction the system should evolve. In limiting dispersal among microclimates, landscape fragmentation impaired the potential role of microclimate in buffering climate change impact on populations. Moreover, fragmentation on its own could induce climatic modifications (Foley *et al.*, 2005). In forest habitat, fragmentation changes the thermal environment by increasing solar radiation at the edge of the patches (Murcia, 1995; Chen *et al.*, 1999; Laurance, 2004). As a consequence, remnant patches become often hot-

ter, drier and with more variable climatic conditions (Murcia, 1995; Chen *et al.*, 1999; Laurance, 2004). The climatic consequences of fragmentation could affect all biological levels, from individuals to ecosystems (Tuff *et al.*, 2016). Landscape fragmentation may thus modify the role of microclimates in species response to climate change.

Finally, landscape structure induced different selective pressures on the phenotypes. We observed that selective gradients and differentials could act on phenotypes in opposite directions depending on the landscape structure (Chapter 3). However, we did not study how these landscape-driven selective pressures could interact with climate-driven selective pressures. As developed earlier in this discussion, traits often correlate into syndromes and selection could act on these syndromes (e.g. Cote *et al.*, 2017). Different syndromes, related to behaviors (Sih *et al.*, 2012), dispersal (Legrand *et al.*, 2016; Cote *et al.*, 2017) and pace-of-life (Goulet *et al.*, 2017; Brans & De Meester, 2018) could be under different selective pressures. Some traits, involved in different syndromes could be under multiple selection pressures induced by multiple drivers. Depending on the direction of these pressures, the traits could evolve fast if the different selection pressures go in the same direction. Conversely, evolution of the trait could be slowed down if selective pressures go in opposite directions. Evolution of the trait will thus depend on the relative strength of the different selective pressures. In the particular case of climate change and habitat fragmentation, it could be possible to disentangle the different pressures using our experimental system. Indeed, the Metatron could allow to add four other combinations of treatments to test for the influence of connectivity in homogeneous climatic conditions (pairs of connected and isolated present-day climate enclosures and warm climate enclosures). However, such fully crossed design experiment could be hard to achieve on large animals such as lizards due to technical constraints (number of enclosures needed, total number of animals). In that case, microcosm experiment in laboratory conditions could help tackle these questions (see Appendix A).

2 Conclusion, limits and perspectives

Through three years of climatic and connectivity manipulations on lizard populations as well as model development, this PhD thesis aimed at understanding the role of dispersal in population responses to climate change. Both experiments and theoretical models underlined the importance to consider dispersal when studying the effects of climate change on biodiversity. We provided new evidence that dispersal is a complex and non random process, where phenotypes and environment interact to shape movement decisions. We demonstrated that considering dispersal as random could lead to wrong predictions on its role in population adaptation and its interaction with phenotypic plasticity and evolutionary adaptation. Predictions of future species distribution were also strongly affected by how dispersal was considered; models considering dispersal as random could strongly overestimate species extinction under contemporary climate change. All these results regarding dispersal highlighted the strong influence that landscape structure and habitat fragmentation could have on species response to climate change. By hampering individual movements, modifying dispersal and subsequent gene flow, habitat fragmentation should affect the two responses to climate change that are range shift and change in population phenotypic composition. Whereas the evidences of population extinctions in response to climate change is growing (Urban, 2018), habitat fragmentation could precipitate the loss of biodiversity by hindering adaptive dispersal. This PhD thesis contributes to the comprehension of the interacting effect of climate change and habitat fragmentation on biodiversity, and call for further studies in that domain to better capture the complexity of population responses to anthropogenic disturbances.

The present work provided a mechanistic view on species responses to climate change. Our experimental approach allowed to measure selective pressures, phenotypic plasticity and dispersal over three years. We did not observe strong selective pressures, on average, on the thermal traits that we studied, in particular in isolated populations. Selection on multiple years can be hard to identify. Previous studies demonstrated that the longer the observational period was, the weaker selection was (Hendry & Kinnison, 1999; Hoekstra

et al., 2001; Schoener, 2011). Selection could be fluctuating or acting with different intensities among the years. It could then be complicated to detect a global trend. However, if directional selection linked to climate acts on a trait, the longer the observational period is the higher the probability to observe the pattern of selection should be. Therefore, longer studies could help detect global selective trends on traits. The duration of our study might fall in the gap between very short studies allowing to detect one year selective pressures and long term studies allowing to detect global directional trends. Moreover, longer studies could help understand the long lasting effect of climate change on populations and better understand how phenotypic plasticity promotes or hinders evolutionary adaptation over time.

Experiments on species with shorter generation time, could also make easier the observation of evolutionary responses to climate change by allowing to follow populations on more generations than we could do with lizards. However, shorter generation time often correlates with higher population density. It could make it difficult to monitor individuals through time and thus to distinguish between the processes incurring population responses. Tackling the same questions with different organisms could also allow us to generalize the conclusions. Using different clades, with different evolutionary history, different life cycles or different dispersal modes might be useful to make reliable predictions on the different groups. Modeling approaches could also help better understand the influence of different species characteristics on their response to environmental perturbations.

Our experimental approach also underlined the potential influence of landscape structure on species response to climate change. We considered two extreme types of landscape structure, one where dispersal was impossible and one where dispersal was allowed. Habitat fragmentation has multiple facets (see Figure 2 in Fahrig (2003) for example) and can affect dispersal pattern in many different ways, depending on the size of the remaining habitat, its shape and the distance separating him from other suitable habitats (McInerny *et al.*, 2007; Martin & Fahrig, 2016). Our experimental system did not allow us to explore many types of landscape structure. Alternative systems could be more appropriate to tackle such questions. For example, in laboratory conditions, it could be easier

to manipulate the distance among habitats, the viscosity of the matrix or the size of the habitats. The system described in Appendix A, using *Tetrahymena thermophila* inhabiting interconnected patches could be modified to increase landscape complexity (e.g. increase distance among patches). Models could also be very useful as they allow to build very complex landscapes to test how landscape configuration modulates species responses to climate change.

The combination of approaches that we used allowed us to highlight important mechanisms in the responses of species to climate change and to predict their consequences over larger spatio-temporal scales. However, it is insufficient to make reliable predictions on the future of specific species in the face of anthropogenic global change. Parameters on population compositions and landscape structure could be extracted from studies on natural populations. These parameters could be used in our model to predict the future distribution of the species under climate change, in integrating the mechanisms of dispersal that we highlight in our experiments. Moreover, merging the monitoring of natural populations with our experimental approach could allow to identify which processes uncovered in the experiment are acting in natural populations. Natural populations of common lizards are being monitored for almost 30 years in the Cévennes mountain. For instance, this long term study allowed to demonstrate that climate change increased individual body size (Chamaillé-Jammes *et al.*, 2006) and released particular trade-offs, that may accelerate pace of life (Rutschmann *et al.*, 2016). The results that we obtained in our experiment support their findings. Further comparisons could help design new experiments, or explain pattern observed in natural populations. For instance, Massot *et al.* (2008) observed a decrease in juvenile dispersal in parallel to the rise in temperature. In the light of our results, we can expect that this reduction in dispersal could affect population dynamics and composition and have future consequences on the relative influence of phenotypic plasticity and evolutionary adaptation.

In the near future, further analyses on the data coming from our experiment on lizard could focus on traits covariation and syndromes. As already developed earlier in this discussion, traits often covary and selective pressures could act on these syndromes by

acting on single traits or on many traits simultaneously. The climatic conditions could favor or disrupt combinations of phenotypic, physiological and life-history traits related to the pace-of-life syndrome (e.g. Brans & De Meester, 2018), or the thermal type (e.g. Goulet *et al.*, 2017). Landscape structure may interact with the climatic conditions to shape these syndromes. Syndromes related to dispersal could be selected in connected habitat compared to isolated ones (see Appendix B). The analyses of the traits used in the first two chapters of this thesis altogether might shed light on global patterns of population differentiation regarding trait combinations. It could also help better understand the selective conflicts related to climatic conditions and landscape structure acting on the traits.

Moreover, as a first step, we focused on the influence of climatic conditions on life-history-traits and thermal phenotypes as we expected these particular traits to be strongly affected by climate change in ectotherms. However, climate change is also expected to strongly affect the physiology of the organisms. The stress induced by warm climatic conditions could be observed at the cellular and molecular level (e.g. heat stress). The study of stress hormones or telomere length could give important information on individuals' state of health in the difference climatic conditions. For instance, telomere length gives information on the level of ageing of the individuals at the molecular scale. As individuals had faster pace-of-life in warm climatic conditions, we expected their telomere to be shorter than for individuals living in present-day climatic conditions. A part of the genetic samples that we have is going to be used to analyze telomere length of each individual between the different treatments.

Looking at the molecular level can also improve our ability to detect microevolutionary processes as it is not limited to a group of phenotypic traits measured. For instance genomic data could be used in association mapping analyses in order to link phenotypic variations to genotypic variations (Franks & Hoffmann, 2012). Development of methods based on the analyses of single nucleotide polymorphisms (SNPs), could also identify climate-related changes in alleles frequency at the genomic scale. By comparing sequences in different populations/conditions, it is possible to identify outliers represent-

ing the markers diverging between populations. Locating loci on a reference genome allows to identify the genes concerned by SNPs variation and to look at their function in order to relate it to phenotypic variations (e.g. Prunier *et al.*, 2011; Franks & Hoffmann, 2012). Comparing populations from present-day and warm climatic conditions might revealed population differentiation and genetic adaptation to the climatic conditions in presence and absence of gene flow. Selection pressures derived from landscape structure could also be investigated at the molecular level. To do so, the genetic samples collected during the experiment are being sequenced.

Finally, a recent study highlighted the consequence of climate change on gut microbiota of common lizard over one year of climatic treatment and the potential consequences for lizards' survival and conditions as well as climate-dependent lizards diet (Bestion *et al.*, 2017). From 2015 to 2018, we also sampled cloacal bacteria of all adult and yearling individuals. Using metabarcoding, we could identify operational taxonomic unit (OTUs) and measure gut composition and diversity. The analyses of these data may help understand how the gut changed through time in response to climate change, and how connectivity and dispersal shape its composition and bacterial diversity. Bestion *et al.* (2017), in a one year experiment, detected the first negative impacts of climatic conditions on microbiota, while on the long run, changes in microbiota may help lizards to deal with changing thermal conditions (Alberdi *et al.*, 2016). For instance, changes in gut composition under cold conditions could modify phenotypes of the host by increased intestinal absorptive capacity (Chevalier *et al.*, 2015). Under climate change, gut modification could thus affect the individual ability to persist.

Besides data analysis, the model that has been developed in this thesis could be used as a basis for further development. Indeed, the current model integrates only a continuous landscape. Whereas our observations underlined the importance of landscape structure on population responses to climate change, complex landscape structure has to be integrated in our model for further investigation on large spatiotemporal scales. For instance, fractals allow to build virtual landscapes in which habitat loss and habitat fragmentation (i.e. habitat aggregation) can be independently manipulated (e.g. Martin

& Fahrig, 2016). We already developed such model, using a species with simplified life cycle (one stage only, non-overlapping generations). Dispersal algorithm has also been modified compared to the previous model. We used stochastic movement simulator (SMS (Palmer *et al.*, 2011)). This algorithm allows to model each step of the dispersal process (emigration, transience and settlement). At each time step, individuals can emigrate, and then move into the landscape via a step by step process, where at each step it can decide to settle. We modified emigration and immigration rules to allow matching habitat choice. Interestingly, preliminary analyses in continuous landscape gave similar results to the ones obtained in Chapter 4, meaning that our results are robust against life cycles, and how dispersal is modeled. In a next step, the landscape structure has to be manipulated to understand how it interacts with random dispersal and matching habitat choice to shape species persistence under climate change.

All of these perspectives will allow to have a better understanding on how climate change affects species, how selective pressures shape phenotypes and how population responses are dependent of landscape structure. With the work presented in this manuscript, we contribute to the global knowledge on species response to contemporary global change. Further analyses will be needed to have a precise understanding on the mechanisms involved in these responses. From this understanding will depend the future of biodiversity, as it will determine future conservation plans and could help alert policy-makers on the importance to consider ecology, in its political definition, as the main objective of their decisions rather than infinite economic growth in a finite world.

6 Appendices

A Influence of landscape structure and genetic diversity on population adaptation to warm temperature: a microcosm experiment

The following appendix describes an experiment that has been realized during my PhD thesis in collaboration with Staffan Jacob, Delphine Legrand, Michèle Huète, Robin Aguilée and Julien Cote at the Theoretical and Experimental Ecology Station in Ariège. The objectives and the general methods of this experiment are presented here.

The aim of the study was to test how landscape structure and genetic diversity influence population adaptation to local climatic conditions. We used *Tetrahymena thermophila* as a model species. *Tetrahymena thermophila* is a ciliate protozoa unicellular species inhabiting water ponds in Northern America. Its reproduction is mainly asexual, with sexual recombination occurring between compatible lines in very stressful conditions. Regarding the conditions of our experiment, reproduction was only asexual (Collins, 2012). At 23°C, the generation time is on average 8 hours and is temperature dependent. As every ectotherm species, *Tetrahymena*'s physiology and performance depend on external temperature, and the link between temperature and physiology is described by thermal performance curve (Huey & Stevenson, 1979). The different lines of *Tetrahymena thermophila* vary in their thermal performance curve (thermal optimum and tolerance). The

different lines could thus be either generalists or specialists and prefer different temperatures.

Here, we built 2-patch systems (5ml eppendorf tubes) connected with a 5 cm long silicon tube with 4mm internal diameter and filled with growth media (see Chaine *et al.*, 2010). We built 12 combinations of treatments (Figure 6.1), replicated eight times each; two temperature treatments (23 and 35°C), two connectivity treatments (isolated and connected systems) and two genetic diversity treatments (4 and 12 genotypes). Temperature in patches was manipulated using dry bath systems placed in incubators. In isolated conditions, the corridors between the two patches were closed by crushing them with plastic clamps. From a pool of 20 genotypes, we formed 16 mixes, 8 with four genotypes/lines and 8 with twelve genotypes/lines. Each mix was distributed in all the combinations of climatic and connectivity treatments.

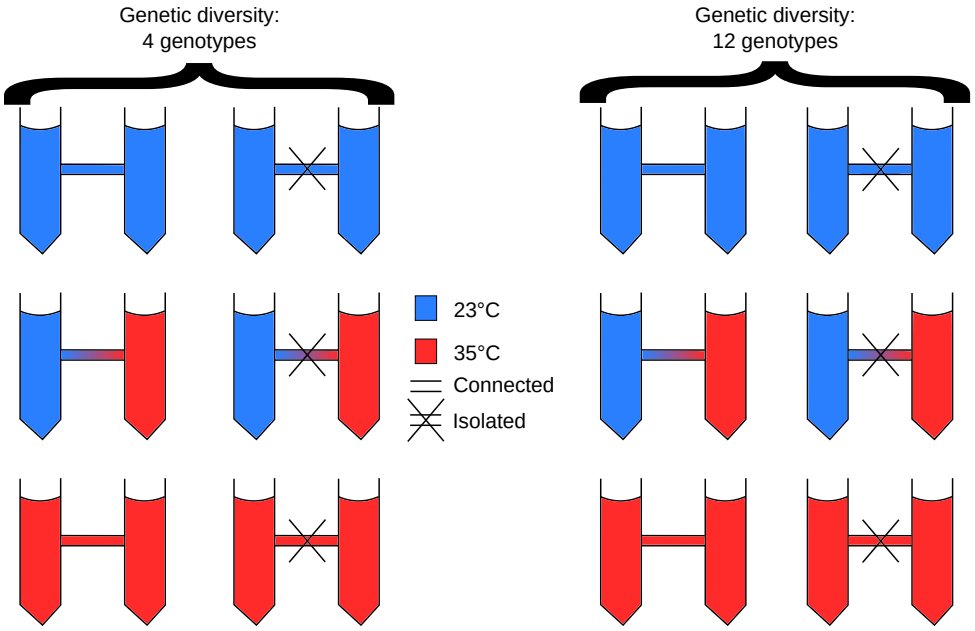

Figure 6.1 – Experimental design

Populations were initially introduced into each patch by inoculating the different mixes of genotypes at a concentration of 20 000 cells/ml. Within a system, the two patches contained the same mix. Then we let the populations evolve in the systems for 5 days, corresponding to 15 generations at 23°C and more at 35°C. We followed density in each patch through time by counting the number of cells on counting slides (Kima precision cell,

five samples of 10 μL per patch) and taking digital pictures under dark-field microscopy. Cell density was measured based on an automatic analysis of pictures using IMAGEJ software (Schneider *et al.* (2012), see Jacob *et al.* (2018)).

At the beginning of the experiment, and after 5 days of treatments, we performed two parallel measurements:

1. We sampled cells by transferring 10 μL of each patch into 96-well plates containing 240 μL of growth media. The samples were reared at 8 different temperatures into incubators (11, 15, 19, 23, 27, 31, 35 and 39°C). Twice a day, we followed population growth rate by measuring population density into each well of the 96-wells plates (Optic density (DO) measurement) for two weeks. Using growth rate at each temperature, we constructed thermal performance curve of each population before and after the experimental treatments. By comparing the thermal performance curve of each population before and after the experimental treatments, we could observe if temperature had an influence on thermal optimum of populations and if the presence of dispersal, and genetic diversity could influence temperature related change in thermal performance curve.
2. We isolated 20 cells per patch into 96-wells plates and reared them at both temperatures (23 and 35°C). Their growth rates were followed through time using DO measurement. The aim was to quantify the variability in growth rate into each population at the different times of the experiment to see how the initial variation was maintained through time.

At the end of the experiment, populations of each patch were split and reared at two different temperatures (23 and 35°C) in isolated conditions in a reciprocal common garden design. After two days, we measured the growth rate of each sub-population at the temperature in which they were maintained during the common garden experiment. Comparing their growth rate before and after the common garden could allow us to determine if the differences induced by our 5 days of treatments were maintained through the common garden, and thus, if they were due to phenotypic plasticity or evolutionary adaptation.

In comparison with the experiment on common lizard, the present experiment was developed to study population response to climate change and habitat fragmentation over many generations. It also made possible the manipulation of genetic diversity to tackle its role in adaptation. Moreover, asexual species might respond differently to environmental pressures than sexual species. The comparison between our two experiments could be a good opportunity to generalize our results and highlight the singularities of the different clades. Finally, as in lizards, *Tetrahymena thermophila* has been showed to disperse non-randomly. Individuals are indeed able to choose their habitat depending on the match between their thermal phenotype and the local climatic condition (Jacob *et al.* (2017), matching habitat choice). Matching habitat choice should promote population differentiation and local adaptation to temperature in connected systems (Jacob *et al.*, 2017). Habitat fragmentation should therefore hinder local adaptation. However, the genetic diversity could also strongly influence the adaptation patterns. We indeed expected populations to better adapt when genetic diversity is high than when it is low because the probability that a given genotype had a thermal optimum matching the local temperature is higher when genetic diversity is high. For the same reason, matching habitat choice could also be influenced by genetic diversity. Matching habitat choice, and subsequent adaptive gene flow, should be favored by genetic diversity. The spatial segregation of genotypes/phenotypes through dispersal according to the match between phenotype and climate should indeed depend on the presence of genotypes/phenotypes matching the local temperature in both patches. If any phenotype matches the local temperature, dispersal decisions will be sub-optimal.

B How landscape structure shapes dispersal syndrome?

Landscape structure may induce changes in population phenotypic distribution by inducing selective pressures on phenotypes. For instance, traits related to dispersal should be affected by landscape structure as habitat fragmentation is predicted to reduce emigration probability (Travis *et al.*, 1999). Previous studies demonstrated that landscape structure can select for traits related to dispersal (e.g. emigration probability (Bonte *et al.*, 2006; Schtickzelle *et al.*, 2006), wing shape (Taylor & Merriam, 1995), body size (Thomas *et al.*, 1998; Hill *et al.*, 1999)). Whereas the traits associated to dispersal often covary under syndromes (Clobert *et al.*, 2009; Ronce & Clobert, 2012; Cote *et al.*, 2017), landscape structure may affect the distribution of individuals on a low to high dispersive continuum.

Here we explored the influence of landscape structure (isolated versus connected habitats) on morphological and behavioural traits related to dispersal, and tested if its effect varied with the climatic conditions.

Methods

We followed populations of the common lizard (*Zootoca vivipara*) inhabiting the Metatron, an experimental system where both climatic conditions and landscape structure were manipulated for 3 years (see general methods for details). We built pairs of enclosures, one with a present day climatic condition and one with a warm climatic condition. Within pairs, populations could be either connected (i.e. the corridor between the two enclosures was open) or isolated (i.e. no connection between the two enclosures). During the three years of experiment, we followed morphological and behavioural traits distribution related to dispersal within each population. Once a year, we measured tibia length, femur length, leg width (adults and yearlings only), tail width (juveniles only), prospecting behavior and activity (adults and yearlings only) of each individual.

Morphology

In May of each year, we measured leg morphology in adults and yearlings, using a calliper (0.1 mm of precision). All individuals were measured for their right posterior leg. Femur length was measured from the groin to the knee, following the femoral pores. Tibia length was measured from the top of the knee to the base of the hand. Leg width was measured on a sagittal plane, in the middle of the thigh.

Because of their small sizes, we used a different method to measure leg morphology in juveniles. Three days after birth, juveniles were softly maintained between two petri dishes and placed under binocular magnifier at x6.5 magnification. A circular lamp set at 10% of illuminance and fixed on the magnifier provided constant light conditions. A ventral picture of the posterior legs was taken with a camera fixed on the top of the magnifier. Pictures were then analyzed using imageJ software (Schneider *et al.*, 2012). We defined three segments, one for femur length (from the groin to under the knee), one for tibia length (from under the knee to the base of the hand) on the right posterior leg and one for the tail width (tail width measured on a coronal plane at a distance of 8 scales from the cloaca).

Behaviour

Adults and yearling individuals were tested for two behavioural traits, activity and prospecting behaviour. To measure prospecting behaviour, individuals were positioned in a terrarium (17x34x20 cm) separated in 3 parts of equal surface by movable plastic separations. Lizards were maintained in the left side of the terrarium with a cardboard as shelter for one night at 18°C. This zone was considered as the "home" zone. The rest of the terrarium was considered as the "new" zone. At 8:30 AM a light bulb (25 W) allowed lizard to thermoregulate. 30 minutes before the test, lights were turned off. Then a light bulb was turned on above the opposite part of the terrarium (i.e. the new zone) and the movable separation was removed. Tests were recorded by camera and lasted 10 minutes. Videos were analyzed using The Observer 2.01 software. From these videos, we extracted the time spent by each lizard in the different zones of the terrarium (home and new),

the time spent to walk in each zone and the time at which the lizard first entered in the new zone. All these variables were summarized into a PCA analysis, with the first axis representing prospecting behavior.

To measure activity, we used data from two different tests. We extracted the time spent by each lizard walking and scratching in the test described in the previous paragraph and in another test used to measure individual sociability (not described here). The different variables were summarized with a PCA analysis, with first axis representing activity.

Statistical analysis

We analyzed juveniles separately from adults and yearlings, hereafter encompassed in the term "adults". For both juveniles and adults, we used PCA analysis to summarize the different correlated variables into syndromes. In adults, the first axis represented morphology and the second axis represented behaviour (Figure 6.2). In Juveniles, since we did not assess the behaviour we only used first axis representing morphology (Figure 6.3).

To explore the influence of our experimental treatments on traits distribution we used linear mixed model with PCA axes as dependent variables. Independent variables included connectivity treatment, climatic conditions, time and the three-way interaction. Only the linear effect of time was considered. We only used data after at least one year of treatment and therefore excluded the data at time 0 from the analyses. Covariables included body size, sex, age stages (adults only), and birth date (juveniles only). Juveniles were measured only one time, at birth, whereas adults could be measured multiple times during their life, once per year. Random intercept thus included individual identity for analysis on adults. It also included enclosure identity to account for the dependency of individuals of the same population, and family identity for analyses on juveniles as sibs from the same clutch were not independent.

Model selection was performed using the following procedure. Full models with all fixed variables and random effects were built and random structure of each model was selected by AIC, following Zuur et al. 2009. Random structure (including structure without random effect) minimizing AIC was then selected. All possible models with fixed

effect were built and ranked by AIC and conditional estimates, standard errors, z-value, relative importance and p-value of all variables present in best models within a delta AIC of 2 were obtained through model averaging procedure (Burnham *et al.*, 2011). All analyses were performed using R software version 3.4.3 (R Core Team, 2017) with lme4, ade4 and MuMin packages.

Results

In both juveniles and adults, we observed that landscape structure affected the combination of traits that we measured. Indeed, individuals had bigger legs in connected populations than in isolated populations (Figure 6.4, 6.6, Table 6.1, 6.2). Moreover, adult individuals prospected more and were more active in connected populations than in isolated populations (Figure 6.5, Table 6.1). These results highlighted the presence of a syndrome, which was affected by landscape configuration. This syndrome is assumed to be related to dispersal, but this assumption remains to be tested. The difference between isolated and connected populations observed in adults increased through time (mostly for behaviour, Table 6.1, Figure 6.5) and was also observed in juveniles after 2 years of treatment (Table 6.2, Figure 6.6).

The climatic conditions also affected morphology of adults and juveniles but less than habitat structure, and this effect was time-dependent (Table 6.1, 6.2). Adults had indeed bigger legs in warm climate than in present-day climate at the end of the experiment, mostly in connected populations (Figure 6.4). Conversely, juveniles had bigger legs in present day climate than in warm climate at the end of the experiment, mostly in isolated populations (Figure 6.6).

Conclusions

These first results seemed to demonstrate that connectivity among habitats promoted combinations of traits related to higher dispersal ability. The difference in leg size between the two connectivity treatments was already observed at birth at the end of the experiment, meaning that developmental plasticity alone could not explain the observed

pattern. Further analysis could relate individual phenotypes/syndrome to their survival probability and reproductive success in order to distinguish between evolutionary adaptation and phenotypic plasticity. If evolutionary adaptation plays a significant role in the development of bigger legs and more active/prospecting behaviours in connected than in isolated populations, and that these traits actually promote dispersal, it will be, to our knowledge, the first evidence of dispersal evolution related to landscape structure in a vertebrate species over very short time scale.

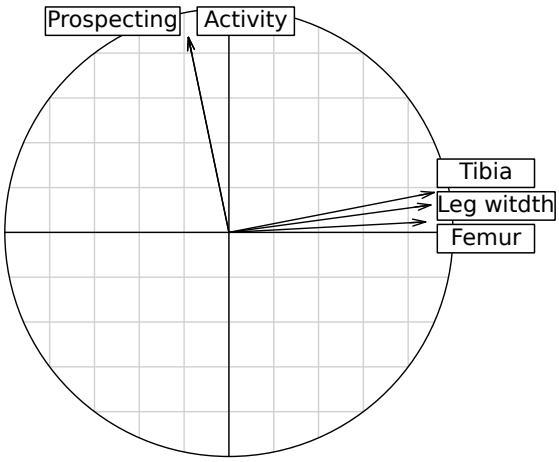

Figure 6.2 – PCA analysis of adults. The first axis (horizontal) represented 50% of the initial variance, and the second (vertical) 31%

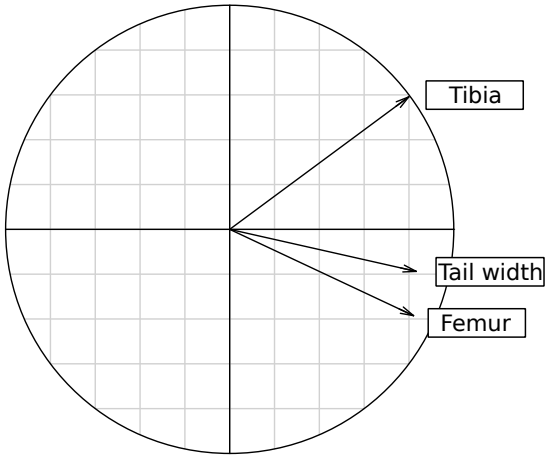

Figure 6.3 – PCA analysis of juveniles. The first axis (horizontal) represented 67% of the initial variance, and the second (vertical) 18%

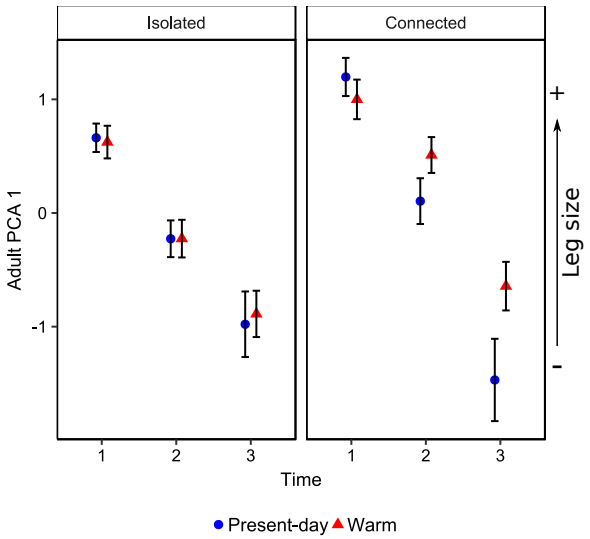

Figure 6.4 – First axis PCA of adults as a function of time in connected and isolate populations of present-day (blue circles) and warm (red triangles) climatic conditions. Mean ± SE are represented

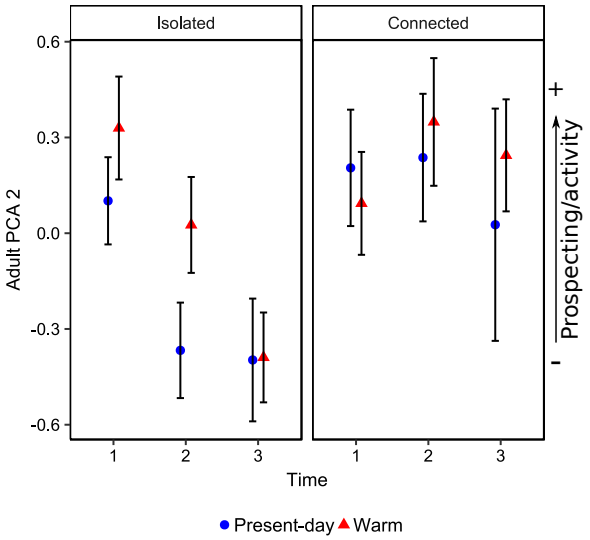

Figure 6.5 – Second axis PCA of adults as a function of time in connected and isolate populations of present-day (blue circles) and warm (red triangles) climatic conditions. Mean ± SE are represented

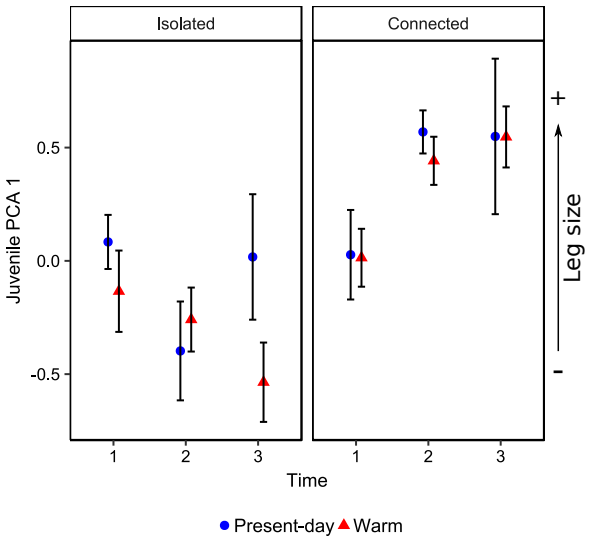

Figure 6.6 – First axis PCA of juveniles as a function of time in connected and isolate populations of present-day (blue circles) and warm (red triangles) climatic conditions. Mean ± SE are represented

Variable	Estimate	SE	z-value	P-value	RI
Adult - ACP axis 1 (morphology)					
Intercept	-0.63	0.11	5.8	<0.001	1
Age	-0.64	0.09	6.81	<0.001	1
Time	-0.65	0.06	11.83	<0.001	1
Body size	0.89	0.05	17.86	<0.001	1
Sex	1.52	0.07	23	<0.001	1
Climate	0.07	0.12	0.56	0.574	0.64
Connectivity	0.26	0.12	2.12	0.034	1
Time*Climate	0.13	0.06	2.08	0.037	0.64
Time*Connectivity	0.1	0.22	0.47	0.636	0.18
Adult - ACP axis 2 (behavior)					
Intercept	-0.55	0.1	5.31	<0.001	1
Age	0.25	0.09	2.62	0.009	1
Time	-0.26	0.06	4.53	<0.001	1
Sex	0.63	0.1	6.15	<0.001	1
Connectivity	0.27	0.1	2.59	0.010	1
Time*Connectivity	0.23	0.09	2.39	0.017	1
Climate	0.14	0.1	1.4	0.163	0.49

Table 6.1 – Statistical models for leg morphology and behavior of adults

Variable	Estimate	SE	z-value	P-value	RI
Juvenile - ACP axis 1 (morphology)					
Intercept	-0.56	0.25	2.25	0.024	1
Time	-0.26	0.09	2.87	0.004	1
Birth date	-0.28	0.06	4.91	<0.001	1
Body size	0.3	0.06	5.14	<0.001	1
Sex	0.6	0.09	6.94	<0.001	1
Connectivity	0.56	0.31	1.79	0.074	1
Time*Connectivity	0.51	0.12	4.13	<0.001	1
Climate	0.22	0.3	0.72	0.472	0.51
Time*Climate	-0.19	0.12	1.6	0.109	0.28

Table 6.2 – Statistical models for leg morphology of juveniles

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Contemporary climate change is leading to population extinction, range shift and composition changes. Dispersal shapes these two last responses by allowing colonization of new habitats and by affecting population composition through gene flow. Depending on its adaptiveness, dispersal can promote or hinder local adaptation and modify the relative influence of phenotypic plasticity and evolutionary adaptation in population phenotypic change. However, landscape fragmentation hampers dispersal, affecting both population responses to climate change, and modifying the relative influence of the different processes involved in these responses. The aim of this PhD was to understand how population responses to climate change could be influenced by landscape fragmentation and by dispersal. By monitoring lizards inhabiting experimental populations where both climatic conditions and connectivity among them were manipulated, we demonstrated that connectivity among populations buffered climate change effects on population dynamics and phenotypic composition. We found that dispersal decisions depended on multiple intrinsic and extrinsic factors allowing to reduce the influence of warmer climate on population dynamics, but decreasing population density in cooler climate. Surprisingly, we also found that dispersal could modify the strength and direction of climate-dependent selection pressures on phenotypes. As a consequence, selection and dispersal acted in synergy to counteract the plastic response of the individuals. When integrated into a model, similar adaptive dispersal behavior strongly altered predictions of species persistence under climate change. We indeed found that adaptive dispersal promoted species range shift and reduced extinction probability compared to a model where dispersal was random (i.e. independent of intrinsic and extrinsic factors). Rather than considering dispersal as a neutral process, our results highlighted the importance to consider it as a complex mechanism shaped by multiple factors and able to drive population responses to climate change. Our results further suggest that fragmentation could strongly increase the influence of climate change on populations and may therefore precipitate their extinction. We thus call for a better integration of dispersal and landscape structure when studying population responses to climate change.

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Titre : Réponses des espèces aux effets combinés du réchauffement climatique et de la fragmentation de l'habitat : le role central de la dispersion
Directeurs de thèse : Jean-Louis Hemptinne, Julien Cote et Robin Aguilée
Lieu et date de la soutenance : Université Paul Sabatier, le 12 Mars 2019

Le changement climatique actuel entraine l'extinction de populations ainsi que des changements dans leur aire de répartition et leur composition. La dispersion impacte ces deux dernières réponses puisqu'elle permet de coloniser de nouveaux habitats de influence la composition des populations au travers du flux de gènes. En fonction de son adaptativité, la dispersion peut promouvoir ou réduire l'adaptation locale et modifier l'importance relative de la plasticité phénotypique et de l'adaptation génétique dans le changement de composition phénotypique des populations. Cependant, la fragmentation du paysage entrave la dispersion, affectant les deux réponses des populations au réchauffement et modifiant l'influence relative des différents processus impliqués dans ces réponses. Le but de cette thèse était de comprendre comment les réponses des populations au changement climatique pouvaient être affectées par la fragmentation du paysage et la dispersion. En suivant des populations de lézards distribuées dans un système expérimental permettant de manipuler simultanément les conditions climatiques et la connectivité entre habitats, nous avons démontré que la connectivité réduisait les effets du réchauffement sur la dynamique et la composition des populations. Nous avons observé que les décisions de dispersion étaient influencées par des facteurs intrinsèques et extrinsèques permettant de réduire l'influence d'un climat plus chaud sur la dynamique des populations, mais en réduisant également la densité des populations en climat plus froid. Etonnamment, nous avons aussi trouvé que la dispersion pouvait modifier la force et la direction des pressions de sélections agissant sur les phénotypes. Les actions conjointes de la dispersion et de la sélection contrebalançaient ainsi la réponse plastique des individus. En les intégrant dans un modèle, des décisions de dispersion adaptative similaires avaient une forte influence sur la persistance prédite des espèces face au réchauffement. En effet, nous avons démontré que la dispersion adaptative favorisait le changement d'aire de répartition des populations et réduisait leur risque d'extinction, en comparaison à un modèle avec dispersion aléatoire (indépendante de facteurs intrinsèques et extrinsèques). Plutôt que de considérer la dispersion comme un processus neutre, nos résultats soulignent l'importance de la considérer comme un mécanisme complexe, façonné par de multiples facteurs et capable de déterminer les réponses des espèces au changement climatique. Nos résultats suggèrent que la fragmentation pourrait fortement augmenter l'influence du changement climatique sur les populations et précipiter leur extinction. Nous appelons donc à une meilleure intégration de la dispersion et de la structure du paysage dans les études sur les réponses des populations au changement climatique.

Mots-clés : Changement climatique, fragmentation du paysage, dispersion

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Discipline administrative : Biologie des populations, écologie

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